### Fulani Knowledge of the Ecological Impacts of *Khaya* senegalensis (Meliaceae) Foliage Harvest in Benin and its Implications for Sustainable Harvest<sup>1</sup>

Orou G. Gaoue<sup>2,3,4,\*</sup> and Tamara Ticktin<sup>2</sup>

<sup>2</sup>Botany Department, University of Hawaii at Manoa, 3190 Maile Way, Honolulu, HI 96822, USA

<sup>3</sup>Laboratoire d'Ecologie Appliquee, Universite d'Abomey Calavi, 01BP 526, Cotonou, Benin

<sup>4</sup>Department of Biology, Institute of Theoretical and Mathematical Ecology, University of Miami,

1301 Memorial Dr., Coral Gables, FL 33146, USA

\*Corresponding author; e-mail: ogaoue@bio.miami.edu

Fulani Knowledge of the Ecological Impacts of Khaya senegalensis (Meliaceae) Foliage Harvest in Benin and Its Implications for Sustainable Harvest. An improved understanding of how local people view their impacts on the resources they exploit and how they perceive that their resources are affected by other factors can provide insight into reasons some resources are overexploited and into strategies to conserve them. In West Africa, various tree species are heavily harvested by indigenous herders for foliage to feed their cattle. The reported declines in populations of several of these species have both biological and cultural implications, as cattle are an integral part of indigenous cultures and livelihoods. In this study we investigated Fulani herders' practices, knowledge, and perceptions of the ecological impacts of harvesting foliage of African mahogany, Khaya senegalensis, in Benin, and we tested some of the factors that may influence them. Fulani herders have detailed ecological knowledge of their impacts on the resources they depend on, and this is finely tuned to local ecological conditions. This knowledge is also widely spread across different sectors of Fulani communities and is highly congruent with scientific findings. However, due to the open-access context of K. senegalensis populations, detailed knowledge of sustainability does not translate into sustainable practices. Fulani perceptions of threats to populations differ significantly between ecological regions and provide key insights for locally relevant resource management plans. Traditional Fulani practices such as the sopoodu provide a basis for sustainable management of proposed Fulani-owned K. senegalensis plantations. This study illustrates how the assessment of local ecological knowledge, practices, and perceptions can play a key role in the design of culturally-appropriate conservation plans.

**Key Words:** Benin, conservation of tropical trees, Fulani, local ecological knowledge, non-timber forest products, harvesting impacts.

#### Introduction

How people perceive of and manipulate their environment and what factors influence these perceptions and interactions are central questions in ethnoecology. Similarly, understanding the social drivers of resource use is also a key question in conservation biology (Bawa et al. 2004; Milner-Gulland 2008). This includes gaining an understanding of local ecological knowledge (LEK) and perceptions, how they are created, factors that affect their distribution across communities, and how they shape resource use practices (Berkes and Folke 2002; Ghimire et al. 2004). In addition, recent ethnoecological studies advocate an integration of LEK and ecological studies to advance our understanding of ecological processes, improve ecological impact assessments, and develop better plans for sustainable resource use (e.g., Bawa et al. 2004; Donovan and Puri 2004; Fraser et al. 2006; Ghimire et al. 2004; Huntington 2000; Ticktin and Johns 2002). To enable such integration, it is important to analyze LEK, evaluate its congruence with available scientific findings (e.g.,

<sup>&</sup>lt;sup>1</sup>Received 19 January 2009; accepted 7 July 2009; published online 25 July 2009.

Barrera-Bassols et al. 2006; Fraser et al. 2006; López-Hoffman et al. 2006), and identify key ideas that can be incorporated into scientific research and sustainable resource use plans.

There has been an increasing effort to describe the LEK related to a variety of plant (e.g., Donovan and Puri 2004; Ghimire et al. 2004; López-Hoffman et al. 2006) and animal species (e.g., Fraser et al. 2006; Huntington 2000; Nabhan 2000), as well as of ecological processes (e.g., Barrera-Bassols and Toledo 2005; Nabhan 2000). These works have documented detailed LEK of the species or system in question and demonstrated that socioeconomic factors such as gender, age, ethnicity, and professional specialization can influence LEK (Case et al. 2005; Gemedo-Dalle et al. 2005; Luoga et al. 2000; Müller-Schwarze 2006). However, in most cases they have not addressed LEK and perceptions of the species and/or ecosystems' responses to disturbance, such as harvest. An improved understanding of how people view their impacts on the resources they exploit and how they perceive that their resources are affected by other factors can shed light on why some resources are overexploited-or not-and on strategies to conserve them.

With increasing drought and grazing pressure, savanna systems in West Africa are experiencing an increasing reduction in availability of grass and trees (Scoones 1995). Frequent seasonal bush fires further reduce the availability of herbaceous fodder in pasturelands dominated by annual grasses. As a consequence, in parts of Benin, Niger, Nigeria, Burkina Faso, Senegal, and Cameroon, various species of trees are heavily and increasingly harvested by indigenous Fulani people as sources of fodder (Gaoue and Ticktin 2007; Gautier et al. 2005; Kristensen and Balslev 2003; Lykke 2000; Petit 2003). The reported decline in populations of several of these species (Lykke 2000; Lykke et al. 2004) has both biological and cultural implications, as cattle are an integral part of Fulani culture and livelihoods. In addition, many of these species are subject to additional uses by loggers and farmers. Sustainable management and conservation of these common pool resources require an understanding of local ecological knowledge and perceptions of the impacts of harvest and other sources of disturbance, and how these influence resource use patterns. This information is critical for designing and implementing management plans that fit with local cultural practices and perceptions.

We employ an ethnoecological framework to explore this issue through a case study of Fulani herders' knowledge, practices, and perceptions of the ecological impacts of harvesting foliage of Khaya senegalensis (Desr.) A. Juss. in Benin. In previous research we documented the ecological impacts of foliage harvest on K. senegalensis population structure and dynamics and how they differ between the dry Sudanian and the moist Sudano-Guinean regions of Benin (Gaoue and Ticktin 2007, 2008). Here, we address the following questions: (1) What ecological knowledge do Fulani harvesters have of the impact of foliage harvest on K. senegalensis reproductive performance, foliage productivity and quality, germination, and population viability? (2) What factors (age, lifestyle [sedentary vs. transhumant], herd size) predict Fulani knowledge of the impacts of K. senegalensis foliage harvest? (3) Do Fulani employ any practices that may reduce the ecological impacts of foliage harvest? (4) What perceptions do Fulani harvesters have of threats to K. senegalensis, and what management actions do they feel are needed to use the species sustainably? (5) Are ecological differences between the dry Sudanian versus moist Sudano-Guinean regions reflected in differences in Fulani harvesters' knowledge and perceptions between these two regions? Based on our results, we compare Fulani knowledge and perceptions of the impacts of harvesting K. senegalensis to scientific findings and discuss the implications of Fulani ecological knowledge for sustainable harvest and long-term persistence of common pool fodder species in a complex social-ecological system.

#### Methods

#### STUDY SPECIES

Khaya senegalensis (Desr.) A. Juss. is one of the most important mahogany species in Africa, distributed in Sudano-Zambezian and Sahelian regions. K. senegalensis is naturally widespread from Senegal to Uganda and Sudan (Arbonnier 2000; Keay 1989). The species is called kaye or kahi (Fulani—West Africa), madacci (Hausa— Northern Nigeria), gbira (Bariba—Benin), and kail or khaye (Wolof—Senegal) in various African languages. The Wolof and Fulani names (khaye or kahi) give the name to the genus, of which this was the first described species (Dalziel 1937).

Khaya senegalensis is a semideciduous tree that grows up to 30 m high and up to 3 m in girth, with a dense crown and short bole covered with dark gray scaly bark (Keay 1989). The bark is bitter and yields gum when wounded. The bitterness of the bark inspired the Hausa name *madacci* (*dacci* meaning bitter), and it is used medicinally throughout the West Africa to treat various diseases including malaria, gastrointestinal diseases, and anemia (Arbonnier 2000; Keay 1989). Leaves are composed of 3–4 pairs of leaflets, 5–10 cm long by 2.3–5 cm broad, more or less elliptic (Keay 1989).

#### STUDY SYSTEM

This study was conducted in the Republic of Benin (6°-12°50' N and 1°-3°40' E), West Africa. Benin covers 114,763 km<sup>2</sup> and is located in the "Dahomey Gap" (Salzmann and Hoelzmann 2005), the dry corridors made mainly of savanna, which split the African rainforest block into two parts. The climate is dry, with subhumid Guineo-Congolean (6°25-7°30 N), Sudano-Guinean (7°30–9°30 N) and Sudanian (9°30–12° N) regions. The vegetation in the Dahomey Gap is characterized by the absence of tropical rainforest, a low percentage of dense semideciduous forest, and the occurrence of savanna through the coast. Khaya senegalensis is distributed in the Sudano-Guinean and Sudanian regions. The Sudanian region is drier, with 900-1,100 mm annual rainfall, and the active vegetation period (145 days) is shorter than in the Sudano-Guinean region (200 days, annual rainfall = 1,100-1,300 mm). Khaya senegalensis is found mainly in gallery forest in the Sudanian region, while in the Sudano-Guinean region, it is also found in woodlands and dry forest.

The Fulani are an ethnic group in West Africa who specialize in cattle husbandry and traditionally migrated throughout the region to obtain green pasture and water for their herds. They usually live in compounds (wuro), which are grouped to form small-sized village camps (gah). Although many Fulani have started growing food crops (e.g., corn, sorghum), cattle serve as a mark of cultural identity and represent the most important assets of the Fulani family (Bierschenk and Forster 2004; Petit 2003). The most important product the Fulani get from their herds is kossam (cows' milk), which is sold by Fulani women, and serves as the source of daily cash income for the family. Part of the kossam is usually kept in the wuro to make and sell cheese

or butter. It may also be mixed fresh to make a tasty corn or sorghum-based porridge (boiri), which is regularly consumed by Fulani and offered to visitors (Bierschenk and Forster 2004; personal observation). Fulani may occasionally sell part of their herd to raise cash for major expenses such as weddings, baptisms, and seasonal celebrations or for buying equipment. To feed cattle and ensure constant milk production, Fulani men prune K. senegalensis during the early dry season (tchedu) and then later prune Afzelia africana Sm. or Pterocarpus erinaceus Poir. These species are also harvested for their timber by logging companies. The majority of Fulani are now sedentary, having settled and developed small-scale farms. However, during the dry season, some Fulani transhumant groups migrate with their livestock from neighboring countries (Niger, Burkina Faso, and Nigeria) to the Sudanian region and then move southward into the Sudano-Guinean region.

During this research, we worked both with sedentary and transhumant Fulani groups who exploit fodder trees from the same lands. In fact, Fulani, loggers, and farmers all harvest K. senegalensis products (foliage, timber, and bark, respectively) from the same lands, including protected and nonprotected areas. Most of the harvesting from protected areas is illegal; although logging and limited grazing may take place in certain protected areas under management plans, most protected areas formally restrict access to all user groups. Khaya senegalensis on nonprotected areas tends to be open to all the user groups, even though farmers in most cases claim property rights. Sometimes farmers give permission to Fulani or loggers to harvest trees, but unauthorized timber harvest and pruning often takes place on these lands as well.

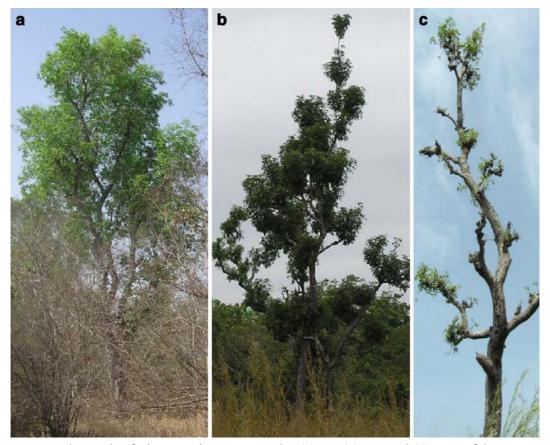
#### Fulani Knowledge of Tree Responses to Foliage Harvest

To assess Fulani ecological knowledge of responses to pruning *K. senegalensis* at the tree and population levels, we carried out semistructured interviews with a total of 45 Fulani men and 10 non-Fulani men. We focused only on men because they are the ones involved in pruning activities. To identify whether Fulani living in different ecological regions have different knowledge and perceptions of *K. senegalensis* response to harvest, we selected participants both

in the Sudanian (dry) and Sudano-Guinean (moist) regions. We interviewed people in 12 gah in the Sudanian region and 27 gah in the Sudano-Guinean region, for a total of 30 Fulani harvesters (15 sedentary and 15 transhumant) in the Sudano-Guinean region and 15 in the Sudanian (12 sedentary and 3 transhumant). The lower number people interviewed in the Sudanian region was due to the fact that at the time of year we conducted the interviews, many Fulani had already moved with their herds southward to greener areas. To test if Fulani age, lifestyle (sedentary or transhumant), and herd size influence their knowledge and perceptions of K. senegalensis, we recorded these variables for each participant. In each gah, we first contacted the local Fulani chief to explain the objectives of our research and to obtain permission to stay and talk with Fulani in the

gah. Participants were selected after informal group interviews to determine if the informant was involved in pruning activities. We also used the snowball method to identify more participants (see Bernard 1995).

To understand Fulani knowledge of the ecological impacts of heavy pruning, in the semistructured interviews we presented each participant with three photographs of *K. senegalensis* trees pruned at 0%, 50%, and 100% removal of their crowns (Fig. 1). The participants were asked to compare fruit and flower production, to comment on the chance that seed produced (if any) would germinate, and to compare the quantity and quality of foliage between trees represented in the three photographs. Based on their responses, we asked further details of how they thought the species would respond to various harvesting intensities.



**Fig. 1.** Photographs of *Khaya senegalensis* trees pruned at (**A**) 0%, (**B**) 50%, and (**C**) 100% of their crown. These photographs were used to investigate Fulani knowledge of the impacts of pruning on fecundity, fertility, and quality, and quantity of foliage produced (see Methods).

In the semistructured interview we also asked participants about the resilience of K. senegalensis to harvest in terms of recovery time, or the number of years after harvest required for a tree to flower and fruit. We asked them to free-list the drivers of K. senegalensis decline in their region as well as actions (including traditional management practices) that they thought would be appropriate to take to ensure its persistence. We asked participants about how much and how often they pruned, and also how much and how often they thought K. senegalensis should be pruned to allow trees to flower and fruit. Finally, to gain further understanding of Fulani harvest practices, knowledge, and perceptions, we also accompanied Fulani herdsmen on 20 different transect walks (see Alexiades 1996) over a period of three years.

To understand the ecological knowledge at *gah* level, and cross-check responses given for each of our questions during the semistructured interviews, we also conducted 12 focus group discussions (four in the Sudano-Guinean and eight in the Sudanian region to make up for the lower number of participants). Each focus group discussion was conducted with three to seven male participants. In these discussions we sought to understand Fulani perceptions of the threats faced by fodder trees in the region, their preferred fodder tree species, different stakeholders in the harvesting system, and potential conflicts between stakeholders.

We also used semistructured interviews with ten non-Fulani farmers, five in each region, and informal interviews with many nongovernmental organization (NGO) workers, state foresters, and local agriculture development agents to get their perspectives of the impact of pruning on the long-term persistence of *K. senegalensis*. Interviews with Fulani herders and farmers were either carried out in Fulfulde or Bariba; interviews with other participants were carried out in French.

#### DATA ANALYSIS

We used a 2-sample Wilcoxon test to test if knowledge of *K. senegalensis* minimum fruiting age, recovery time after heavy pruning, time-toextinction, and current and sustainable pruning frequencies varied between Fulani living in the two different ecological regions. To understand how Fulani knowledge of the ecological impacts of heavy pruning affects their decision-making, we ran Spearman rank correlation tests between Fulani estimations of recovery time, time to extinction, and minimum fruiting age, and their perceptions of sustainable pruning frequencies and the probability that trees fruit after harvest.

To test if the factors listed by our participants as the main threats to K. senegalensis persistence were independent of their ecological region, we used Fisher's exact test instead of a chi-square, because some cells of our contingency table had frequencies less than five (Crawley 2007). We used simple logistic regression to test if the probability that a Fulani reported that pruning reduces K. senegalensis fruiting or seed germination, or improves foliage quality and quantity (each of these was considered a dependent variable), is affected by participant's age, lifestyle, herd size, and ecological region in which he operates (independent variables). All the analyses were done in R. 2.7.0 (R Development Core Team 2008). For the logistic regression, we used a glm function with a binomial distribution function for each of the dependent variables and a logit link function (Crawley 2007).

#### Results

#### FULANI ECOLOGICAL KNOWLEDGE OF FOLIAGE HARVESTING IMPACTS

# Impact of Harvest on the Quantity and Quality of Foliage

Fulani knowledge of the effects of pruning on K. senegalensis foliage quality and quantity was not influenced by the ecological region where they operated, their age, life-style, or herd size (Table 1). According to 95% of the Fulani participants we interviewed, pruning improves both the quality and quantity of leaves trees produced. They explained that pruning rejuvenates the trees, removes old leaves, and allows trees to produce new light green shiny leaves that are preferred by cattle to the old dark green leaves. They said that a lack of pruning over many seasons may attract parasites; therefore, the more one prunes a tree, the better leaves it will produce the following year. However, participants did mention that repeated pruning at high levels such as in Fig. 1c would weaken the tree, preventing it from renewing its branches, or lead to the production of smaller leaves in the long-term.

TABLE 1. LOGISTIC REGRESSION TESTING THE EFFECT OF ECOLOGICAL REGION, AGE, ETHNIC GROUP, AND HERD	
SIZE OF FULANI PARTICIPANTS ON THE PROBABILITY THAT THEY SAID PRUNING REDUCES KHAYA SENEGALENSIS	
CHANCE OF FRUIT AND SEED GERMINATION, AND IMPROVES QUALITY AND QUANTITY OF FOLIAGE.	

	Fruit	ting	Quality	oliage Quantit		foliage	Germination	
	Z	p-value	Z	p-value	Z	p-value	Z	p-value
Intercept	-0.373	0.710	0.151	0.880	0.415	0.678	-0.902	0.366
Region	-0.007	0.994	0.004	0.997	0.007	0.994	-3.166	0.001**
Age	0.403	0.687	0.652	0.514	0.802	0.422	0.991	0.321
Ethnicity	-0.541	0.588	-0.459	0.647	-1.601	0.109	0.106	0.915
Herd size	-1.077	0.281	0.475	0.635	0.830	0.407	2.234	0.025*

\*\* p < 0.001; \* p < 0.05. Other *p*-values are nonsignificant (p > 0.05).

#### Impact of Harvest on Fruiting Probability, Production, and Seed Germination

According to 80% of the Fulani participants we interviewed, pruning does not affect whether a K. senegalensis tree will fruit or not. The probability that a participant said pruning affected the chance that a tree fruits was not influenced by participant age, lifestyle, herd size, or ecological region (Table 1). Twenty percent of participants responded that only heavy pruning (100% crown removal) affects fruiting probability. In both ecological regions, Fulani explained that pruning intensity (percent branches pruned) matters less than pruning frequency (number of times a tree was pruned) as the most important factor in determining the probability of fruiting. They maintained that even trees pruned at 100% are likely to produce flowers and fruit in the future, if given enough time to recover.

Fulani in the drier Sudanian region reported significantly longer recovery times after 100% foliage harvest (3.5 years) than those in the Sudano-Guinean region (2 years; W=69.5, p < 0.0001, Fig. 2a). In both cases, participants said that the recovery time will be longer for higher pruning intensities.

In addition, Fulani reported that the number of fruits produced decreases with increasing pruning intensity. The reduction in fruit production was perceived as a consequence of a physical reduction in the number of plant structures that could bear fruit (e.g., leafy branches) or leaf age/ maturity. Fulani explained that a tree cannot produce fruits unless its foliage has had time to mature. Leaves were considered as the "machine" that produces flower and fruits. Participants argued that branches with young, newly-produced leaves (due to lack of maturity) or very old leaves (due to parasite attacks) would not bear fruits even if they produced flowers.

Fulani reported that *K. senegalensis*' reproductive response to harvest varies not only with the frequency and intensity of harvest, but also with the age of the tree. Older trees tend to take more time to recover from harvest than younger trees. Fulani in the Sudanian region reported that trees reach reproductive size by 7 years, while those in the Sudano-Guinean region reported a minimum fruiting age of 16.5 years. This difference in perceptions between regions was significant (W= 458, p<0.0001, Fig. 2b). Fulani in both regions reported that heavily harvested trees take 2–3 more years to reach fruiting size than nonharvested trees.

Fulani views on whether pruning reduces seed germination rates (defined by Fulani as the chance that seeds produced will give rise to seedlings) differed significantly between the two ecological regions and were also influenced by participant's herd size (Table 1). The majority of participants (75%) in the Sudanian region said that pruning does not reduce seed quality or the probability of germination. According to some participants (22%) in the Sudanian region, old leaves on old trees may produce "bad seeds"; therefore, pruning may even improve seed quality if done less frequently. In contrast, in the Sudano-Guinean region, the majority (84%) believed that heavy and persistent pruning weakens the trees and may reduce seed quality and germination rates. In both regions, participants with more cattle tended to say that heavy pruning had more of an effect on seed quality and germination rates (Table 1).

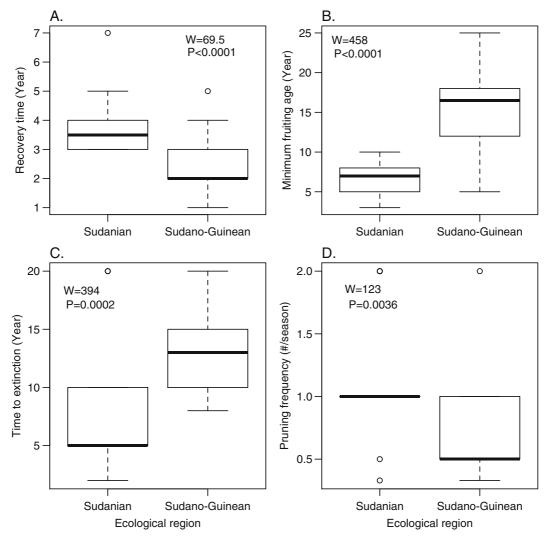


Fig. 2. Variation in Fulani knowledge of *Khaya senegalensis* between the Sudanian and Sudano-Guinean regions of (A) minimum fruiting age, (B) recovery time after heavy harvest, (C) time-to-extinction, and (D) sustainable pruning frequency.

#### Impact of Harvest on Khaya senegalensis Population Viability

The study participants all reported that K. senegalensis is going extinct in their region. Estimates of time to extinction ranged between 2 and 20 years. By "extinction," participants were referring to the disappearance of K. senegalensis individuals that can still be pruned in their region. In most cases this refers to K. senegalensis populations located outside of the protected areas because they do not have the rights to prune populations inside the protected areas. Fulani in the dry Sudanian region predicted that *K. senegalensis* will go extinct within 5 years, about twice as fast as predicted by participants in the Sudano-Guinean region: 13 years (W=394, p=0.0002, Fig. 2c). The participants who said that *K. senegalensis* would go extinct faster also stated that the species would take a longer time to recover after a heavy harvest (r=-0.372, p= 0.0108) and would fruit at an older age (r= 0.492, p=0.0005).

#### FULANI MANAGEMENT PRACTICES TO REDUCE HARVESTING IMPACTS

There is a traditional practice pertaining to limiting pruning intensity and locally referred to in the Fulani language as *sopoodu* or *oloodu*, which means "head" or "top" (Fig. 3a). The sopoodu practice consists of leaving a few branches unpruned at the tops of trees. This practice is specific to K. senegalensis and not found in any other fodder species. Participants provided four main reasons to explain why someone would resist pruning all the branches and leave a sopoodu; most participants listed more than one reason. One of the reasons (reported by  $13\pm5\%$ of participants) is to show courage and skill. K. senegalensis, unlike other fodder tree species, is tall (up to 30 m height) and difficult to climb. Pruning K. senegalensis is therefore a dangerous activity that provides opportunities for young Fulani to demonstrate their talents, and therefore to earn respect and prestige from their peers.

Fulani participants also explained that the *sopoodu* is spared to "protect the tree and allow it to grow in height and to reproduce." The majority

of participants  $(60\pm6\%)$  who suggested this believe that removing the *sopoodu* would stop tree growth. They also compared the *sopoodu* to the square of hair that is commonly left on Fulani children head, which is also referred to by the same name (Fig. 3c).

Some participants  $(21 \pm 3\%)$  said that the *sopoodu* carries special spirits known in Fulfulde as "*djin*." Traditionally, harvesters leave the *sopoodu* to avoid disturbing those spirits, which would hunt them down if angered. Others suggested that the *sopoodu* is spared to avoid leaving the tree "naked." The reasons provided by Fulani were not significantly different across the two ecological regions (Fisher's exact test; p=0.2392).

We also found that most trees had small *sopoodu*, and in some cases the *sopoodu* may even disappear (Fig. 3b), indicating the loss of this management practice. According to Fulani participants, "the size of the *sopoodu* tells a lot about the personality of the harvester." They associated the small-sized or no*sopoodu* with young and inexperienced harvesters, and with immigrant Fulani harvesters who care less about the regeneration of the species.

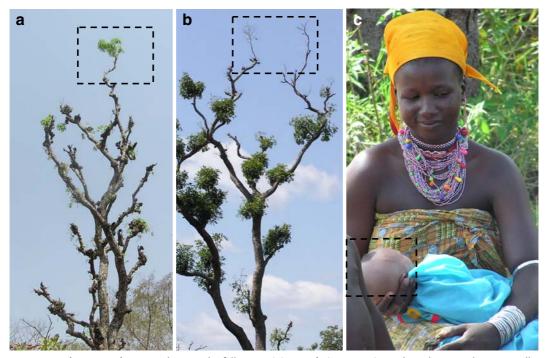


Fig. 3. *Khaya senegalensis* tree showing the following: (A) *sopoodu* (see square): top branches spared intentionally by Fulani to protect the tree, allow growth and reproduction. (B) The *sopoodu* is not always present. (C) Fulani mother, Adama, with her newborn showing the *sopoodu* (square patch of hair on the head).

#### THREATS TO KHAYA SENEGALENSIS PERSISTENCE

The three main stakeholder groups who use K. senegalensis are logging companies, farmers, and Fulani. According to 69% of Fulani participants, the K. senegalensis population has been declining over time due to logging and agriculture. Only 19% of the Fulani participants suggested that pruning is directly threatening the persistence of the species (Fig. 4a). They harvest K. senegalensis more frequently and at a higher intensity than before because logging and land clearing have reduced the density of the trees in their region. In turn, workers in logging companies complained that Fulani-by making notches on the trunk of trees to climb them-reduce the quality of the timber. The farmers we interviewed complained that Fulani herders take cattle onto their farms to browse not only K. senegalensis foliage but also their crops (yams, cotton, and corn). As a consequence, some farmers cut down K. senegalensis trees on their farms to avoid attracting Fulani herds.

The main drivers of the decline of *K. senegal*ensis suggested by participants significantly differed between ecological regions (Fig. 4a). In addition to logging and land clearing, participants in the dry Sudanian region considered bush fire and trunk debarking for medicinal purposes as other threats to *K. senegalensis* survival in their region. A greater number of participants in the Sudanian region free-listed heavy pruning as a threat than in the Sudano-Guinean region.

### How to Promote the Long-Term Persistence of *Khaya senegalensis*?

The Fulani we interviewed free-listed a few actions necessary to ensure the persistence of *K. senegalensis* in their region (Fig. 4b). The most important step, they suggested, was for NGOs to help promote the planting of *K. senegalensis* by Fulani themselves, through training and assistance in establishing nurseries and planting the species. Study participants also suggested that the govern-

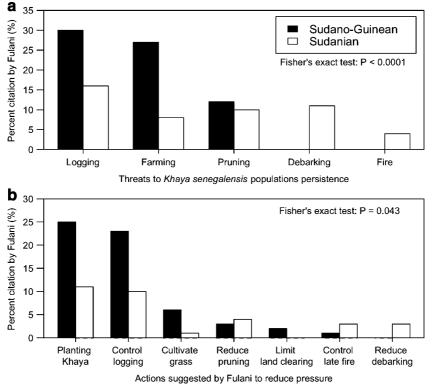


Fig. 4. (A) Main drivers of *Khaya senegalensis* population decline identified by Fulani participants, and (B) actions suggested by Fulani to reduce the pressure on *Khaya senegalensis* in two ecological regions of Benin: Sudano-Guinean (closed bars) and Sudanian regions (open bars).

ment must play its part in cracking down on logging companies that are mainly responsible for the decline of *K. senegalensis* in their region.

A few Fulani (8%) suggested regulating pruning intensity and frequency as part of the package of actions to reduce pressure on the species. Those who suggested regulating pruning suggested a maximum harvest limit of 25-50% of foliage pruned every two or three years in the Sudano-Guinean region. In the Sudanian region, participants did not mention any specific percentage canopy pruning that would be necessary for sustainability, but emphasized reducing the pruning frequency per tree. Fulani in the Sudanian region suggested a significantly shorter interval between harvests to ensure sustainability (median: once per season) than those in the Sudano-Guinean region (median: once every two seasons (W=123, p=0.0036; Fig. 2d).

However, most of the participants said that reducing the intensity and/or frequency of pruning is generally an unrealistic solution to the decline of *K. senegalensis* population size. They said that the density of the species is so low now that it will be impossible to reduce pruning frequency. In fact, Fulani from both regions reported similar current pruning frequencies: twice a season (W=185, p=0.1518).

The set of conservation measures proposed by Fulani were consistent with the main threats to *K. senegalensis* persistence that they reported in the free-lists. These were also different between the two ecological regions (Fig. 4b). Fulani in the Sudanian region proposed more actions to limit the effects of wild fire, debarking, and pruning, while in the Sudano-Guinean region participants' suggestions focused on planting more *K. senegalensis* as well as grasses and controlling logging.

#### Discussion

In this study we investigated how Fulani herders understand the dynamics of one the key plant resources with which they interact, *K. senegalensis*. Our results illustrate how information on local ecological knowledge, practices, and perceptions can provide insight on decision-making processes for local resource use and inform locally appropriate sustainable management plans.

#### FULANI ECOLOGICAL KNOWLEDGE OF *KHAYA SENEGALENSIS* HARVESTING IMPACTS

Our interviews revealed that many Fulani have detailed ecological knowledge of the ways in which

their foliage harvesting affects foliage quantity and quality, reproductive behavior, and germination of K. senegalensis and of some of the factors that influence them. Fulani knowledge of harvest impacts is largely consistent with scientific research on this and other species. For example, Fulani observation that pruning improves foliage quantity is consistent with the theory of compensatory growth of plants after defoliation (Anten et al. 2003; Bruna and Nogueira-Ribeiro 2005; Chazdon 1991). Fulani knowledge that trees need time to recover from heavy pruning before they can produce flowers and fruits is consistent with the negative relationship between persistent and heavy defoliation and reproductive success reported for this and other fodder species (Fornara and du Toit 2007; Gaoue and Ticktin 2008). Similarly, Fulani knowledge that pruning improves foliage quality also coincides with scientific research. Pruning of large K. senegalensis trees increases the nitrogen concentration in leaves (Gaoue 2008), and studies on other species have also shown that young leaves contain higher nitrogen concentrations than old leaves due to lignin content (Kitajima et al. 2002). However, chronic defoliation may lead to a reallocation of N from leaves to perennial organs (Fornara and du Toit 2007). This may be the case for K. senegalensis, the pruning of which has been going on for a prolonged period at high rateswith more than 70% of K. senegalensis trees harvested to 100% of their crown (Gaoue and Ticktin 2007). Fulani observations that K. senegalensis is going extinct in their regions coincides with our findings that harvested K. senegalensis populations are projected to decline over the long run in both regions (Gaoue 2008).

Our results also illustrate that Fulani ecological knowledge is finely tuned to local ecological conditions; differences in Fulani knowledge and perceptions between the two ecological regions reflected environmental differences across sites and were highly consistent with ecological findings. Fulani in the drier Sudanian region reported slower recovery times, higher minimum fruiting age, and shorter time to extinction than those in the Sudano-Guinean region, and this coincides with ecological studies showing that the effects of harvest are more severe in the Sudanian region (Gaoue 2008). In addition, in contrast to Fulani in Sudanian region, those in the Sudano-Guinean region reported that pruning negatively affected seed quality and germination rates. This is consistent with ecological findings that harvested

populations in the Sudano-Guinean region (but not the Sudanian region) have significantly lower densities of seedlings than nonharvested populations (Gaoue and Ticktin 2007). Given predictions of increasing aridity and desertification in West Africa (see Nicholson 2001; Paeth and Hense 2004; West et al. 2008), current LEK of Fulani in the drier Sudanian region can provide important insight for future practices of those in the Sudano-Guinean region.

#### Factors Affecting Fulani Ecological Knowledge

Fulani knowledge of the effects of pruning on foliage quality and quantity and on reproduction was not influenced by age, lifestyle, or herd size, suggesting that knowledge is similar across a diversity of Fulani herders. Although similar findings that knowledge may be distributed evenly across different sectors of communities have been reported elsewhere (Kristensen and Lykke 2003; McMillen 2008), other studies have reported important differences across sectors, such as greater knowledge among older people (Case et al. 2005; Gemedo-Dalle et al. 2005; Luoga et al. 2000; Müller-Schwarze 2006). Local ecological knowledge is acquired from long-term observations of ecological processes (Berkes and Folke 2002). Variation in knowledge within and among user groups can be a result of variation in the exposure of each user group to the knowledge, its mode of transmission, and the importance of the knowledge to vital functions (food, medicine, survival). In this case, the similarity in knowledge across age groups may be explained by the fact that young Fulani are heavily involved in pruning activities, even more so than older Fulani.

The finding that herd size influenced perceptions of the impacts of foliage harvest on seed quality and seedling germination may be explained by the longer time Fulani with large herd sizes may have to spend in the field and the higher number of trees they prune to feed their herd. They may have larger impacts on resources but also likely accumulate more experience and develop better knowledge of very specific responses of trees to harvest.

## FULANI PRACTICES TO REDUCE HARVESTING IMPACTS

Fulani have a traditional practice to reduce the impacts of harvest—the leaving of the *sopoodu*.

The practice of *sopoodu* is not unique to the Fulani in Benin; it has been reported among Fulani in northern Cameroon (Gautier et al. 2005) and probably occurs across the whole West African region where Fulani have migrated. The sopoodu practice illustrates the ways in which local people's beliefs, social values, and ecological knowledge shape the way they use their resources. The Fulani provided several reasons, including ecological, social, and spiritual reasons, to explain why they leave the sopoodu, and the same participants gave more than one reason. The ecological explanation provided was that removing the top of the tree would prevent it from growing and ultimately affect fruit production and survival. Indeed damage to *Khaya* spp. shoot apical meristems by other means (e.g., attack by the shoot borer Hypsipyla robusta) leads to forked trees and slow growth (Ofori et al. 2007).

However, the fact that the size and practice of the sopoodu has greatly diminished today likely relates to the disappearance of the cultural and spiritual reasons provided. This is likely a result of changes in cultural beliefs and social values that have occurred at the same time as increasing competition over the reduced pool of common pool resources. K. senegalensis is becoming rare and Fulani now maximize the amount of foliage they harvest when they climb a tree (Gaoue and Ticktin 2007). In addition, many Fulani now embrace Christianity and have abandoned some of their cultural practices that are now considered as sins. Many Fulani interviewed therefore said they do not believe removing the *sopoodu* would anger the djin. Similar changes in, and loss of, local ecological knowledge and taboos related to resource use have been reported elsewhere (Benz et al. 2000; Shanley and Rosa 2004). This poses a challenge for biocultural conservation and the promotion of sustainable resource use based on local knowledge.

#### Relationships between Fulani Knowledge and Harvest Practices

Our results show a discrepancy between current Fulani pruning frequencies of *K. senegalensis* and the frequency that they believe is sustainable. Although most participants thought that *K. senegalensis* should be harvested once per season to allow trees to flower and fruit, they currently harvest trees at least twice a season. This frequency of pruning for *K. senegalensis* has also been reported in the Fulani community of the nearby country of Burkina Faso (Petit 2003). These results emphasize that when "unsustainable" resource harvest takes place, it is not necessarily due to a lack of knowledge of the system or of the ecological implications. Instead, Fulani actions were based on their perceptions of other threats to K. senegalensis. After suggesting sustainable harvesting frequencies, the study participants stressed that these rates are not realistic in the current context, and, instead, they pointed to the competing uses of the species with logging companies and farmers who they believed to be main drivers of K. senegalensis population decline. Many felt that if the government cracked down on loggers and enforced the law that recommends higher tree density on farms, this would improve the density of fodder trees (not only of K. senegalensis but also A. africana and P. erinaceus) and reduce pruning pressure. They felt that even if they did not prune K. senegalensis, it would be logged for timber, and since trees are likely to be logged, the impact of pruning is negligible in the end. Clearly, to understand local resource use practices, especially for common pool species, an understanding of both ecological knowledge and of perceptions of other threats by other user groups is necessary.

#### Implications of Fulani Knowledge and Perceptions for *Khaya senegalensis* Conservation

Khaya senegalensis harvest provides an example of competing uses for an open-access, common pool resource (see Hardin 1968). Khaya senegalensis and other fodder trees on public lands (protected and nonprotected areas) are open access resources for farmers (bark harvesters, land clearing), Fulani (fodder harvest), and illegal loggers (timber harvest). Each party in this social-ecological system tends to maximize their share of the resource. The Fulani we interviewed emphasized that under these circumstances, the species is likely to go locally extinct. However, as suggested by other authors (Burke 2001; Smith and Berkes 1991), privatization of the habitat that harbors these fodder species will not be an ideal solution.

The difference in Fulani perceptions of the main drivers of *K. senegalensis* decline between ecological regions translated into different sets of management suggestions from Fulani in each

region. The shortage of resources and the dryness of the Sudanian region make fire and debarking an additional threat which Fulani in the Sudano-Guinean region did not mention. In the dry region, fire not only accelerates the death of trees that have been seriously debarked, but also removes the little herbaceous (annual) dry pasture available during the dry season. In addition, debarking is more frequent in the Sudanian region (Gaoue and Ticktin 2007).

However, Fulani in both regions emphasized that controlling logging is necessary for maintaining K. senegalensis populations. Regulations on resource use are not well enforced by the forestry administration, and illegal logging is taking place even in some protected areas. Controlling logging could likely also improve the status of other fodder trees such as A. africana and P. erinaceus, which are also logged. One way that logging could be better controlled would be the promotion of government and privately-owned plantations of fast-growing timber species. For example, teak plantations have been common in Benin since late 1940s and have been successful in providing timber. Clearly, to be sustainable new plantations should not involve the conversion of native habitat.

The Fulani in both regions also emphasized the need for programs to plant K. senegalensis. Although K. senegalensis has already been successfully cultivated for timber since the 1950s, these are rarely pruned because the Fulani consider them to be private property (Gaoue and Ticktin 2007). Instead, the establishment of local level and Fulani-owned plantations on Fulani farms and around compounds could be an effective strategy for reducing the pressure on K. senegalensis populations and other wild harvested fodder species. This would convert K. senegalensis in these areas from an open-access to a common-property resource, where informal or formal Fulani rules and regulations on resource use, such as the *sopoodu*, could be enforced. However, given that not all the Fulani own land, this measure will certainly not work for everyone. In Benin, there has been a participatory effort by NGOs, government, Fulani, and farmers to establish migration corridors for dry season transhumance. Planting K. senegalensis to delimit these corridors and also inside the corridor would be another alternative to increase the availability of fodder for both sedentary and transhumant Fulani.

Interestingly, Fulani did not suggest increasing other fodder trees as a strategy to decrease pressure on K. senegalensis in either region. This is likely a reflection of the multicontextual use of K. senegalensis. Fulani use visual cues (e.g., color and glossiness of foliage) to estimate foliage palatability to cattle. Fulani point out that translucent light green leaves are more palatable to cattle than opaque dark leaves, and that the fresh odor that young leaves produce is attractive to their cattle. This use of physical and sensory cues as functional guides is common in many cultural groups (Etkin 1988; but see also Casagrande 2000). However, K. senegalensis foliage is not very palatable to livestock and was rejected by sheep in a browsing experiment in Nigeria (Omokanye et al. 2001; Petit 2003). The foliage is bitter and, in terms of taste, does not constitute the best fodder. Nonetheless, Fulani force their calves to get used to eating K. senegalensis foliage despite the bitterness (see also Petit 2003). They believe that K. senegalensis is a source of nutrients and also a medicine that will allow their cattle to resist disease and survive through the difficult dry season. Our results illustrate how the concept of food-medicine (see Etkin 1988, 2002) can be applied beyond the human context. The multicontextual uses of K. senegalensis as fodder-medicine therefore make it difficult to replace with other species which are popularly suggested for agroforestry, such as Gliricidia sepium and Leucaena leucocephala.

In conclusion, this study illustrates the very detailed ecological knowledge that local people have of their impacts on the resources they depend on and how under open-access conditions, local perceptions of threats to resources may be better predictors than LEK of resource use patterns. It also demonstrates the importance of cross-regional studies of LEK (in this case in arid versus moist regions) for providing insight on how current resource-use practices may need to adapt in the future to climate change. Clearly both LEK and perceptions can play key roles in the development and design of resource management and conservation plans.

#### Acknowledgments

This work was supported by grants from the Beatrice Krauss Fellowship and the Ecology, Evolution and Conservation Biology Program at the University of Hawaii at Manoa. We are grateful to the Fulani communities who participated in this research, to Yacoubou Boni, Samba Tobou Adam, and Rachidi Saliou for field assistance, and Ismail Moumouni, Florent Okry, Shimona Quazi, Nina Etkin, Kim Bridges, Andy Taylor, and Don Drake for useful discussion.

#### Literature Cited

- Alexiades, M. N. 1996. Selected Guidelines for Ethnobotanical Research: A Field Manual. The New York Botanical Garden, Bronx, New York.
- Anten, N. P. R., M. Martinez-Ramos, and D. D. Ackerly. 2003. Defoliation and Growth in an Understory Palm: Quantifying the Contribution of Compensatory Responses. Ecology 84:2905–2918.
- Arbonnier, M. 2000. Arbres, arbustes et lianes des zones sèches d'Afrique de l'Ouest. 2nd edition. CIRAD, France.
- Barrera-Bassols, N. and V. M. Toledo. 2005. Ethnoecology of the Yucatec Maya: Symbolism, Knowledge and Management of Natural Resources. Journal of Latin American Geography 4:10–41.
- , J. A. Zinck, and E. Van Ranst. 2006. Local Soil Classification and Comparison of Indigenous and Technical Soil Maps in a Mesoamerican Community Using Spatial Analysis. Geoderma 135:140–162.
- Bawa, K. S., J. W. Kress, M. N. Nadkarni, and S. Lele. 2004. Beyond Paradise: Meeting the Challenges in Tropical Biology in the 21st Century. Biotropica 36:437–446.
- Benz, B. F., J. E. Cevallos, F. M. Santana, J. A. Rosales, and S. M. Graf. 2000. Losing Knowledge about Plant Use in the Sierra de Manantlan Biosphere Reserve, Mexico. Economic Botany 54:183–191.
- Berkes, F. and C. Folke. 2002. Back to the Future: Ecosystem Dynamics and Local Knowledge. Pages 121–146 in L. H. Gunderson and C. S. Holling, eds., Panarchy: Understanding Transformation in Human and Natural Systems. Island Press, Washington, D.C.
- Bernard, H. R. 1995. Research Method in Anthropology: Qualitative and Quantitative Approaches. Alta Mira Press, Walnut Creek, California.
- Bierschenk, T. and R. Forster. 2004. L'organisation sociale des Peuls dans l'est de l'Atacora, Republique du Benin: Communes de Kouande, Pehonco et Kerou. Institut fur

Ethnologie und Afrikastudien, Johannes Gutenberg Universitat, Mainz.

- Bruna, E. M. and N. B. M. Nogueira-Ribeiro. 2005. The Compensatory Responses of an Understory Herb to Experimental Damage Are Habitat Dependent. American Journal of Botany 92:2101–2106.
- Burke, B. E. 2001. Hardin Revisited: A Critical Look at Perception and the Logic of the Commons. Human Ecology 29:449–479.
- Casagrande, D. G. 2000. Human Taste and Cognition in Tzeltal Maya Medicinal Plant Use. Journal of Ecological Anthropology 4:57–69.
- Case, R. J., G. F. Pauli, and D. D. Soejarto. 2005. Factors in Maintaining Indigenous Knowledge among Ethnic Communities of Manus Island. Economic Botany 59:356–365.
- Chazdon, R. L. 1991. Effects of Leaf and Ramet Removal on Growth and Reproduction of *Geonoma congesta*, a Clonal Understorey Palm. Journal of Ecology 79:1137–1146.
- Crawley, M. J. 2007. The R Book. John Wiley and Sons, West Sussex, England.
- Dalziel, J. M. 1937. The Useful Plants of West Tropical Africa. Academic Press, Crown Agents for the Colonies, London.
- Donovan, D. and R. Puri. 2004. Learning from Traditional Knowledge of Non-timber Forest Products: Penan Benalui and the Autecology of *Aquilaria* in Indonesian Borneo. Ecology and Society 9:3. http://www.ecologyandsociety. org/vol9/iss3/art3/.
- Etkin, N. L. 1988. Ethnopharmacology: Biobehavioral Approaches in the Anthropological Study of Indigenous Medicines. Annual Review of Anthropology 17:23–42.
  - 2002. Local Knowledge of Biotic Diversity and Its Conservation in Rural Hausaland, Northern Nigeria. Economic Botany 56:73–88.
- Fornara, D. A. and J. T. du Toit. 2007. Browsing Laws? Response of *Acacia nigrescens* to Ungulate Browsing in an African Savanna. Ecology 88:200–209.
- Fraser, D. J., T. Coon, M. R. Prince, R. Dion, and L. Bernatchez. 2006. Integrating Traditional and Evolutionary Knowledge in Biodiversity Conservation: A Population Level Case Study. Ecology and Society 11(2):4. http://www.ecologyand society.org/vol11/iss12/art14/.
- Gaoue, O. G. 2008. Assessing the Impact of Bark and Foliage Harvest on *Khaya senegalensis* (Meliaceae) in Benin, West Africa. Ph.D. thesis, University of Hawaii at Manoa, Honolulu.

——— and T. Ticktin. 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.

— and — 2008. Impacts of Bark and Foliage Harvest on *Khaya senegalensis* (Meliaceae) Reproductive Performance in Benin. Journal of Applied Ecology 45:34–40.

- Gautier, D., A. Bonnerat, and A. Njoya. 2005. The Relationship between Herders and Trees in Space and Time in Northern Cameroon. The Geographical Journal 171:324–339.
- Gemedo-Dalle, T., B. L. Maass, and J. Isselstein. 2005. Plant Biodiversity and Ethnobotany of Borana Pastoralists in Southern Oromia, Ethiopia. Economic Botany 59:43–65.
- Ghimire, S., D. McKey, and Y. Aumeeruddy-Thomas. 2004. Heterogeneity in Ethnoecological Knowledge and Management of Medicinal Plants in the Himalayas of Nepal: Implications for Conservation. Ecology and Society 9:6. http://www.ecologyandsociety.org/vol9/iss3/ art6/.
- Hardin, G. 1968. The Tragedy of the Commons. Science 162:1243–1248.
- Huntington, H. P. 2000. Using Traditional Ecological Knowledge in Science: Methods and Applications. Ecological Applications 10:1270–1274.
- Keay, R. W. J. 1989. Tree of Nigeria. Clarendon Press, Oxford, U.K.
- Kitajima, K., S. S. Mulkey, M. Samaniego, and S. J. Wright. 2002. Decline of Photosynthetic Capacity with Leaf Age and Position in Two Tropical Pioneer Tree Species. American Journal of Botany 89:1925–1932.
- Kristensen, M. and H. Balslev. 2003. Perceptions, Use and Availability of Woody Plants among the Gourounsi in Burkina Faso. Biodiversity and Conservation 12:1715–1739.
- López-Hoffman, L., I. E. Monroe, E. Narváez, M. Martínez-Ramos, and D. D. Ackerly. 2006. Sustainability of Mangrove Harvesting: How Do Harvesters' Perceptions Differ from Ecological Analysis? Ecology and Society 11:14. http://www.ecologyandsociety.org/ vol11/iss12/art14/.

- Luoga, E. J., E. T. F. Witkowski, and K. Balkwill. 2000. Differential Utilization and Ethnobotany of Trees in Kitulanghalo Forest Reserve and Surrounding Communal Lands, Eastern Tanzania. Economic Botany 54:328–343.
- Lykke, A. M. 2000. Local Perceptions of Vegetation Change and Priorities for Conservation of Woody-Savanna Vegetation in Senegal. Journal of Environmental Management 59:107–120.
- ——, M. K. Kristensen, and S. Ganaba. 2004. Valuation of Local Use and Dynamics of 56 Woody Species in the Sahel. Biodiversity and Conservation 13:1961–1990.
- McMillen, H. L. 2008. Conserving the Roots of Trade: Local Ecological Knowledge of Ethnomedicines from Tanga, Tanzania Markets. Ph. D. thesis, University of Hawaii at Manoa, Honolulu.
- Milner-Gulland, E. J. 2008. New Perspectives on Harvesting as One Driver of Ecosystem Dynamics. Journal of Applied Ecology 45:1–3.
- Müller-Schwarze, N. K. 2006. Antes and Hoy Día: Plant Knowledge and Categorization as Adaptations to Life in Panama in the Twentyfirst Century. Economic Botany 60:321–334.
- Nabhan, G. P. 2000. Interspecific Relationships Affecting Endangered Species Recognized by O'Odham and Comcaac Cultures. Ecological Applications 10:1288–1295.
- Nicholson, S. E. 2001. Climatic and Environmental Change in Africa during the Last Two Centuries. Climate Research 17:123–144.
- Ofori, D. A., E. Opuni-Frimpong, and J. R. Cobbinah. 2007. Provenance Variation in *Khaya* Species for Growth and Resistance to Shoot Borer *Hypsipyla robusta*. Forest Ecology and Management 242:438–443.
- Omokanye, A. T., R. O. Balogun, O. S. Onifade, R. A. Afolayan, and M. E. Olayemi. 2001. Assessment of Preference and Intake of Browse

Species by Yankasa Sheep at Shika, Nigeria. Small Ruminant Research 42:201–208.

- Paeth, H. and A. Hense. 2004. SST versus Climate Change Signals in West African Rainfall: 20th-Century Variations and Future Projections. Climatic Change 65:179–208.
- Petit, S. 2003. Parklands with Fodder Trees: A Fulße Response to Environmental and Social Changes. Applied Geography 23:205–225.
- R Development Core Team. 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. http://www.Rproject.org.
- Salzmann, U. and P. Hoelzmann. 2005. The Dahomey Gap: An Abrupt Climatically Induced Rain Forest Fragmentation in West Africa during the Late Holocene. The Holocene 15:190–199.
- Scoones, I. 1995. Living with Uncertainty: New Directions in Pastoral Development in Africa. SRP, Exeter, London.
- Shanley, P. and N. A. Rosa. 2004. Eroding Knowledge: An Ethnobotanical Inventory in Eastern Amazonian's Logging Frontier. Economic Botany 58:135–160.
- Smith, A. H. and F. Berkes. 1991. Solution to the Tragedy of the Commons: Sea-urchin Management in St Lucia, West Indies. Environmental Conservation 18:131–136.
- Ticktin, T. and T. Johns. 2002. Chinanteco Management of *Aechmea magdalenae*: Implications for the Use of TEK and TRM in Management Plans. Economic Botany 56:177– 191.
- West, C. T., C. Roncoli, and F. Ouattara. 2008. Local Perceptions and Regional Climate Trends on the Central Plateau of Burkina Faso. Land Degradation and Development 19:289–304.