Fruit Removal and Seed Predation in Two African Trees (*Lannea acida* and *Lannea welwitschii*, Anacardiaceae)

Britta K. Kunz[1]* and K. Eduard Linsenmair[2]

[1] *Institute of Ecology, Evolution and Diversity, Goethe-University Frankfurt, Siesmayerstraße 70, D-60323 Frankfurt am Main, Germany*

[2] *Department of Animal Ecology and Tropical Biology, Theodor-Boveri Institute of Biosciences, Am Hubland, D-97074 Würzburg, Germany*

*Corresponding author; E-mail: b.kunz@bio.uni-frankfurt.de

Abstract

Fruit removal is an important component of plant fitness. The role of different frugivores in removal efficiency of two small-fruited trees, *Lannea acida* and *L. welwitschii* (Anacardiaceae), at Comoé National Park, north-eastern La Cote d'Ivoire was investigated. At least 12 bird species, the red-legged sun squirrel (*Heliosciurus rufobrachium*), and four primate species consumed the fruits of the *L. acida* focal tree. Crop removal efficiency varied between 21% and 30% in two consecutive years. Up to 100% of the harvest and fruit fall were unripe fruits. Removal efficiency in *L. welwitschii* was higher (48.5%) despite lower visitation rates and only two species observed feeding. Most *L. welwitschii* fruits were removed during and after maturation but pre-dispersal seed predation by *H. rufobrachium* left only 19.9% of the total crop to potential seed dispersal. In contrast, *H. rufobrachium* rarely fed on *L. acida* seeds. Sun squirrels consumed about twice (*L. acida*) to 10 times as much (*L. welwitschii*) fruits (seeds) per visit than birds. Primates removed 20-30 times more *L. acida* fruits and about 30 times more *L. welwitschii* fruit per visit than birds, but birds are able to compensate for lower food intake per visit by visiting a feeding tree more frequently. Birds and primates may, thus, both be important seed dispersers of *Lannea* seeds in terms of quantity. As a consequence of a large amount of unripe fruit fall and high pre-dispersal seed predation by vertebrates, the reproductive output of the focal trees during the study period in terms of dispersed seeds was low. Regeneration in *L. acida* and *L. welwitschii* might, thus, be source limited and dissemination limited, at least in certain years. Because interannual and intraspecific variation in fruit removal can be substantial, further research is required to determine long-term reproductive output in the two species.

Introduction

Fruit removal by frugivores is a prerequisite of seed dispersal in animal-dispersed plants and, thus, an important component of plant fitness (Izhaki, 2002). Removal efficiency, i.e. the proportion of the total fruit crop removed from an individual plant, provides a first estimate of seed-dispersal success relative to the number of fruits produced by the plant (Izhaki, 2002). Fruit removal, however, does not necessarily equate effective dispersal (Schupp, 1993). For example, fruits may be removed before maturation of seeds or seeds may be destroyed during consumption. Frugivores can largely differ in the overall amount of fruits they remove from a plant and in the number of seeds they disperse, according to variation in the number of visits made to the plant and the number of fruits removed per visit (Schupp, 1993). Yet, quantitative data, particularly on African tree species and their fruit consumers are rare.

Removal efficiency in the two dioecious trees, *Lannea acida* A. Rich. and *L. welwitschii* (Hiern) Engl. (Anacardiaceae), was investigated. *L. acida* is widespread throughout West African savanna and may also occur along forest edges (Hovestadt, 1997; Arbonnier, 2000). *L. welwitschii*, the only West African forest species in the genus, occurs from La Cote d'Ivoire to Angola, Uganda and Gabon (Hutchinson *et al*., 1954-1968). Fruiting starts at the end of the dry season, or the beginning of the rainy season when trees are leafless, and lasts 1-2 months in both species. The small, single-seeded drupes (*L. acida* 9.6 mm × 8.5 mm, *L. welwitschii* 8.6 mm × 6.8 mm on average) are edible and are clustered in infructescences. Drupes appear dark-purple (*L. acida*) to purple-black (*L. welwitschii*) to the human eye when mature.

In the Comoé National Park (CNP), north-eastern La Cote d'Ivoire, at least 23 bird and five mammal species (the sun squirrel, *Heliosciurus rufobrachium*, and four primate species) feed on fruits or seeds of *L. acida* and, or *L. welwitschii* (Hovestadt, 1997; Kunz *et al.*, 2008). There were no indications of nocturnal fruit consumers (Hovestadt, 1997; Kunz *et al.*, 2008). In the present paper data on the quantitative contribution of the consumers to fruit removal and seed dispersal in both trees have been provided.

Materials an methods

The study site was situated in the south-west of the CNP (08° 30'–09° 36' N, 003° 07'–004° 25' W), north-eastern La Cote d'Ivoire. The vegetation comprises a mosaic of savanna, forest islands and gallery forest and is described in more detail elsewhere (Poilecot, 1991; Hovestadt *et al.*, 1999; Porembski, 2001). The climate is characterized by a dry season from November to March. Mean annual precipitation from January 1994 to December 1999 was 1,053 mm $year^{-1}$.

The CNP harbours a rich flora and fauna. So far, 498 bird species (Salewski, 2000; Salewski & Göken, 2001; Rheindt *et al.*, 2002) and 152 mammal species have been recorded (Poilecot, 1991; Mess & Krell, 1999; Fischer *et al.*, 2000; Fischer *et al.*, 2002). Fruit removal by frugivores in one *L. acida* tree (Laac1) was monitored in 1999 and 2000 and in one *L. welwitschii* tree (Lawe) in 2000. Trees were 13 m and 12 m high; dbh (at 1.20 m) was 66.0 cm and 45.5 cm, respectively. Both trees were situated at the forest edge within 50 m from each other and were chosen with regards to fruiting and good visibility of the crown.

To determine removal efficiency of each tree, the trees' fruit crops was estimated at the onset and end of the study, as well as fruit fall from the trees prior to the onset of the study and during the study. The first crop size estimation took place when crops were unripe (Laac, at 21 March 1999 and 2000) or at the very start of maturation (Lawe, at 14 April 2000). The average fruit number from a minimum of five infructescences was multiplied by the mean number of infructescences from four branches of similar size and the number of equal branches of the tree. Infructescences and branches were selected haphazardly.

Fruit fall prior to study onset was considered by counting the number of fallen fruits in two quadrants (30 cm × 30 cm) randomly placed within each 45° angle beneath the crown and extrapolated the mean fruit number over all quadrants to the crown area projected to the ground (CAG). A tree's CAG was calculated from the area spanned by lines connecting the peripheral points of the tree crown measured at 45° angles from the trunk.

No remarkable activity of fruit consumers in the trees prior to study onset was noted. The number of fruits on each tree plus the fruit fall up to that time was equated with total fruit production. Six 1 m^2-fruit traps, placed randomly under each tree at 1 m height, documented fruit fall throughout the study. The traps were emptied every other day and fallen fruits were categorized as either unripe (green to greenish-purple) or mature (purple to purple-black). Fruits with seeds emptied by squirrels were counted separately, at whatever state of maturity. The mean number of fruits and predated seeds, respectively, were extrapolated to the CAG. Fruit trapping terminated when the crop was reduced to < 5% of its total fruit production or when fruits remaining on the tree desiccated and were no longer attractive to frugivores (Laac1: 21 April 1999 and 5 April 2000, *L. welwitschii*: 12 June 2000).

To obtain data on visitation rates and food intake by frugivores, the trees were observed between 6:00 a.m. and 7:00 p.m. for 3–5 h daily. Observation hours were about evenly distributed across daytime hours. Laac1 was observed during the same period in which fruit trapping took place (63 h in 1999; 53 h in 2000). To increase the number of feeding observations a neighbouring *L. acida* tree (Laac2) was likewise monitored in 1999 for another 45 h. Observations of Lawe started with fruit trapping and ended on 3 May 2000 after constantly low visitation rates (< 2 h^{-1}) had not increased significantly during 3 weeks of observation (totalling 44 observation hours).

Observation distance to all focal trees was about 20 m, observers partly screened from view by other trees. Diurnal non-human primates inhabiting the site were used to the presence of researchers. A tree's crown was scanned every 5 min for 1 min, using binoculars. Identification of foraging species was verified using Mackworth-Praed & Grant (1970–1973); Serle & Morel (1977); Brown *et al.* (1982–1992); Kingdon (1997) and Borrow & Demey (2001).

Further data collection and analyses focused on species that removed entire fruits (in birds: swallowers, which swallow fruits entirely). Each foraging individual seen in a given scan was assessed as one record, and the mean hourly number of records per tree and year calculated.

In between scans, the individuals' length of stay and the number of fruits (seeds) consumed per minute were noted. Removal effectiveness of animal species based on the average number of fruits or seeds consumed per minute, the mean length of stay, and the mean number of feeding visits over all observation hours per tree species were assessed (following Cordeiro *et al.*, 2004). Many primate species occupy large home ranges and infrequently return to the same feeding tree. To increase sample size on food intake and length of feeding stays of primates, data from two habituated olive baboon groups in CNP, and occasional observations of other primate species in *L. acida* and *L. welwitschii* trees, other than the focal ones, were included (Kunz & Linsenmair, 2008; Kunz *et al.*, 2008).

Results

Crop sizes, fruit fall and the total amount of fruit removal from the focal trees Laac1 and

Lawe are displayed in (Table 1). Most fruit fell beneath the crown. Between 82% (Lawe) and 100% (Laac1) of the fruit fall was of unripe fruit. Twelve bird species, the red-legged sun squirrel (*Heliosciurus rufobrachium*) and two primate species were observed feeding on *L. acida* fruits in 1999 (Appendix 1). Removal efficiency of Laac1 in this year was 30%. In 2000, five bird species, the red-legged sun squirrel and three primate species were recorded. Removal efficiency (21%) was lower than in the previous year. In both years, birds visited *L. acida* trees more regularly, and more often per hour than sun squirrels and primates, who, in turn, visited the trees for longer feeding sessions (Table 2). However, birds other than village weavers (*Ploceus cucullatus*), starlings (*Cinnyricinclus leucogaste*r, *Lamprotornis* sp.*)*, common bulbuls (*Pycnonotus barbatus*), and African thrushes (*Turdus pelios*) were rarely observed.

Only *P. barbatus* and *H. rufobrachium* were recorded feeding in Lawe. Broken branches and torn-off infructescences beneath the crown indicated primate feeding visits outside observation hours. Despite the overall low visitation rate, removal efficiency (48.5%) was higher than in Laac1, and most fruits were removed during and after maturation. Yet, seed eating by *H. rufobrachium* accounted for more than half of the total fruit removal from Lawe, corresponding to pre-dispersal seed predation of over one-quarter of the total fruit crop. In contrast, *H. rufobrachium* was rarely observed in *L. acida* (Table 2) and predated seeds did fail to turn up in seed traps in either year. Sun squirrels consumed about two (*L. acida*) to 10 times as much fruits (seeds) (*L. welwitschii*) per visit than birds. Primates removed 20-30 times more *L. acida* fruits and about 30 times more *L. welwitschii* fruit per visit than birds (Table 2).

TABLE 1
Fruit production, fruit fall and fruit removal from L. *acida (Laac1) in 1999 and 2000 and* L. welwitschii *(Lawe) in 2000*

	Laac1 (1999)	*Laac1 (2000)*	*Lawe (2000)*
CAG [m^2]	140.1	134.3	123.5
Fruit fall prior to study onset	60,200	38,100	11,000
Crop size at study onset	187,600	157,500	154,400
Total fruit production	247,800	195,600	165,400
FRUIT fall during study	104,600	113,800	74,200
Total fruit fall*(%)	164,800 (66.5)	151,900 (77.7)	85,200 (51.5)
unripe fruit fall [% of total fruit production]*	65.1	77.7	42
Fruit crop size at end of study	8,200	2,000	10
Removal efficiency [%] (n)	30.2 (74,800)	21.3$^{\#}$ (41,700)	48.5^{x} (80,190)

*: refer to total fruit production including fruit fall prior to study onset; $^{\#}$: all fruits removed were unripe; ^{x}: 59% of the removed fruits (28.6% of total crop) were predated by *H. rufobrachium*

Study periods: Laac1 21 March to 21 April 1999 and 21 March to 5 April 2000; Lawe 14 April to 12 June 2000. Number of fruits estimated to the nearest hundred. CAG: crown area projected to the ground.

TABLE 2

Estimated fruit consumption of bird and mammal species in L. acida and L. welwitschii trees

	Birds				Mammals					
	P. barbatus	*T. pelios*	*sp. Lamprotornis*	*C. leucogaster*	*P. cucullatus*	*H. rufobrachium*	*C . t. lunulatus.*	*C. m. lowei*	*C. petaurista*	*P. anubis*
L. acida										
Mean no. of fruits / min* (± sd)	4.5 ± 1.7	4.5 ± 2.8	1.7 ± 0.5	2.7 ± 2.1	3.1 ± 2.0	3.2 ± 0.8	22.0 ± 7.0	-	19.7 ± 3.5	19.4 ± 7.8
No of observations	47	10	6	32	21	10	22	-	3	$42^{(11)}$
Mean length of stay [min] (± sd)	3.6 ± 2.6	2.3 ± 1.8	-	3.3 ± 2.7	3.1 ± 1.2	11.5 ± 5.9	9.5 ± 5.4	-	12.0 ± 1.4	19.3 ± 14.5
No of observations	53	18	-	15	13	6	6	-	2	$30^{(6)}$
Mean no. of fruits / stay	16.4	10.4	-	8.8	9.8	36.8	209.5	-	236.0	346.1
Laac1										
Mean no. of records / hr (1999 & 2000)	2.30	0.79	-	0.81	1.27	0.09	0.44	0.05	0.02	0.35
Mean no. fruits / observation hr	37.6	8.2		7.2	12.4	3.3	92.1	-	4.7	121.1
Laac2										
Mean no. of records / hr (1999 & 2000)	0.28	0.15	-	0.03	0.88	0.13	0.01	-	-	-
Mean no. fruits / observation hr	4.6	1.5	-	0.3	8.6	4.8	2.3	-	-	-
L. welwitschii (Lawe)										
Mean nº. of fruits / min* (± sd)	3.8 ± 1.3	-	-	-	-	5.9 ± 1.8	-	-	-	28.7 ± 11.9
No of observations	6	-	-	-	-	20	-	-	-	$62^{(0)}$
Mean length of stay [min] (± sd)	4.4 ± 2.1	-	-	-	-	30.3 ± 14.1	-	-	-	16.0 ± 8.1
No of observations	11	-	-	-	-	15	-	-	-	$7^{(0)}$
Mean no. of fruits / stay	16.7	-	-	-	-	177.5	-	-	-	459.8
Mean no. of records / hr	0.54	-	-	-	-	0.41	-	-	-	-
Mean no. fruits / observation hr	9.0	-	-	-	-	72.8	-	-	-	-

* Observations in Laac1 and Laac2 are pooled. When data on fruit consumption included trees other than the focal ones superscript numbers in brackets $^{()}$ indicate number of observations in the focal tree.

Discussion

Fruit removal efficiency in both trees yielded less than 50% of the total crop. Though higher removal rates from woody plants are not uncommon (Ortiz-Pulido *et al.*, 2007), in many animal dispersed tree species most fruits fall below the parents' canopy (Clark *et al.*, 2005). Fruit fallen to the ground may be dispersed secondarily by ground foraging animals (Brewer & Rejmanek, 1999). In both focal trees, however, almost all fruit fall was of unripe fruit. As seeds from unripe *L. acida* and *L. welwitschii* fruits failed to germinate (Kunz *et al.*, 2008), unripe fruit fall in the focal trees presumably has to be considered seed loss.

Twenty-two bird and five mammal species (four primates and the sun squirrel *H. rufobrachium*) were recorded feeding in *L. acida* in previous studies in CNP, compared to 13 birds and the same five mammal species in *L. welwitschii* (Hovestadt, 1997; Kunz *et al.*, 2008,). Shinozaki curves showing the number of frugivorous bird species as a function of an increasing number of observed trees indicate that, like in the present study, generally more species are expected to feed on *L. acida* than on *L. welwitschii* fruits (Hovestadt, 1997). Nevertheless, the total fruit removal from Lawe (48.5%) was higher than from Laac1 (30.2% in 1999 and 21.3% in 2000), suggesting consumer visits to Lawe peaked outside observation hours. Torn-off infructescences and broken branches in fruit traps indicated that this is due partially to infrequent and irregular feeding visits by primates.

Primates generally removed more fruits per feeding visit than birds, but birds are able to compensate for lower food intake per visit by visiting a feeding tree more frequently. Birds and primates may, thus, both be important seed dispersers in terms of quantity. During the study period, however, up to 100% of the fruit removed from Laac1 by birds and primates was unripe fruit and, thus, accounts for seed predation (Kunz *et al.*, 2008). In Lawe most fruits were removed during and after maturation. Seed predation by *H. rufobrachium*, however, accounted for 28.6% of total crop size, leaving only 19.9% to potential seed dispersal.

As a consequence of large amount of unripe fruit fall and the high pre-dispersal seed predation by vertebrates, the reproductive output during the study period in terms of dispersed seeds was low, and in Laac1 in 2000 presumably zero. It was difficult to find *Lannea* trees bearing ripe fruit in 2000 (particularly *L. acida*) for fruit size measurements, indicating that trees other than the focal ones were also depleted early in the fruiting period while crops were unripe. Keeping in mind the small sample size of this study, the data suggest that regeneration in individual *L. acida* and *L. welwitschii* trees may be source limited and dissemination limited (Schupp *et al.*, 2002), at least in certain years. However, interannual and intraspecific variation in fruit removal can be substantial (Izhaki, 2002), and further research is required to determine long term reproductive output in the two species.

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APPENDIX 1

Species observed feeding on fruits or seeds of L. acida *and* L. welwitschii *focal trees in Comoé National Park, Ivory Coast*

	Common name	*Scientific name*	L. acida *1999*	*2000*	L. welwitschii *2000*
Birds					
Musophagidae	Green Turaco	*Tauraco persa*	x		
	Western grey plantain-eater	*Crinifer piscator*	x		
Capitonidae	Yellow-rumped tinkerbird	*Pogoniulus bilineatus*	x		
	Yellow-fronted tinkerbird	*Pogoniulus chrysoconus*	x		
Pycnonotidae	Common bulbul	*Pycnonotus barbatus*	x	x	x
Turdidae	African thrush	*Turdus pelios*	x	x	
Platysteiridae	Senegal batis	*Batis senegalensis*	x		
Sturnidae	Bronze-tailed glossy starling	*Lamprotornis cf. chalcurus*	x		
	Violet-backed starling	*Cinnyricinclus leucogaster*	x	x	
Ploceidae	Village weaver	*Ploceus cucullatus*	x	x	
Fringillidae	Yellow-fronted canary	*Serinus mozambicus*	x	x	
Emberizidae	Cabanis's bunting	*Emberiza cabanisi*	x		
Mammals					
Sciuridae	Red-legged sun squirrel	*Heliosciurus rufobrachium*	x	x	x
Cercopithecidae	White-crowned mangabey	*Cercocebus t. lunulatus*	x	x	
	Lowe's monkey	*Cercopithecus m. lowei*		x	
	Lesser spot-nosed monkey	*Cercopithecus petaurista*		x	
	Olive baboon	*Papio anubis*	x		