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SHORT COMMUNICATION

Episodic severe damage to canopy trees by elephants: interactions with fire, frost and rain

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Elephants (*Loxodonta africana* (Blumenbach 1797)) can have a major transforming effect on savanna structure through felling, debarking or uprooting trees (Dublin *et al.* 1990, Laws 1970, Mapaure & Campbell 2002). However, it is difficult to separate their influence from that of other causes of tree mortality, including wind storms (Spinage & Guinness 1971), drought (Lewis 1991, van de Vijver *et al.* 1999), fire (Higgins *et al.* 2000), and in some situations frost (Childes & Walker 1987, Holdo 2006), especially when interactions among them may occur (de Beer *et al.* 2006, Laws *et al.* 1975, Pienaar *et al.* 1966). Furthermore, the consequences for woodland dynamics depend on the size classes of the trees affected, as well as on how the disturbance is concentrated in time and space. Mortality of canopy trees has a much greater and longer-lasting impact than losses among the regenerating stages of these trees. However, the consequences may be less adverse for ecosystem function and biodiversity if the disturbing effects are locally concentrated, generating a patch mosaic of stands at different stages of regeneration (Remmert 1991).

The observations reported here were obtained fortuitously during a 3-y study aimed at assessing factors governing the selective impact of elephants on woody vegetation in northern Botswana. Routine recording showed that feeding by elephants was concentrated on shrubs or saplings of tree species at levels of utilization that appeared sustainable (Chafota 2007). However, we encountered three situations where numerous big trees had been pushed over by elephants in particular localities. Each occurrence was evidently associated with a different causal influence, and hence unreplicated. Episodic severe damage of this nature is difficult to document within any study of limited duration. Hence we report the patterns observed as examples to be augmented by further observations.

Our study was conducted within a section of Chobe National Park adjoining the Chobe River together with neighbouring forest reserves and hunting concessions. The region is generally underlain by Kalahari sand, and the mean annual rainfall recorded in Kasane town in the north-east is 700 mm, falling mainly between November and March. Extremely high concentrations of elephants develop near the Chobe and Linyanti rivers during the dry season, amounting to 7–12 animals km^{-2} (Craig 1990, Gibson *et al.* 1998). Impacts by these animals have led to the transformation of much of the riparian woodland adjoining the Chobe River into a shrubland with standing dead trunks of the former trees remaining (Mosugelo *et al.* 2002), and a similar process of woodland conversion was apparently underway in the riparian woodland adjoining the Linyanti River further west (Wackernagel 1993).

The first case, associated with the influence of fire, occurred about 30 km south of the Chobe River, on the border between Chobe National Park and Kasane Forest Reserve Extension (location 25°6′E, 18°9′S). Severe tree damage on the forest reserve side of the boundary was discovered in the second week of November 1992, when we tracked movements of elephants away from the river after rain showers had filled pools in the interior. An extensive fire had burned through the forest reserve during the last week of September, but was stopped from penetrating the national park by a fire-break marking the boundary.

The area within the forest reserve where tree felling was evident was sampled within 22 belt transects each 10 m wide × 400 m long located about 200 m apart. Ten transects were sampled similarly on the unburned

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Table 1. Severe damage to canopy trees inflicted by elephants in the Kasane Forest Extension during November 1992 following a fire.

Species	Diameter class (cm)	n	Proportion of trees damaged			
			Uprooted	Stem snapped	Bark stripped > 50%	Overall
Burned site						
Burkea africana	5–10	103	0.08	0	0	0.08
	10–20	181	0.25	0.07	0	0.32
	20–30	111	0.19	0	0	0.19
	30–40	16	0	0	0	0
Colophospermum mopane	5–10	35	0	0.09	0.03	0.12
	10–20	63	0	0.13	0	0.13
	20–30	30	0	0	0	0
	30–40	3	0	0	0	0
	>40	1	0	0	0	0
Brachystegia boehmii	5–10	21	0	0.14	0	0.14
	10–20	6	0	0.33	0	0.33
	20–30	8	0.13	0.25	0	0.38
	30–40	8	0	0.25	0	0.25
	>40	7	0	0	0	0
Unburned site						
Burkea africana	5–10	30	0.07	0.07	0	0.14
	10–20	47	0.19	0.04	0	0.23
	20–30	43	0.05	0	0	0.05
	30–40	14	0	0	0	0
Brachystegia boehmii	5–10	2	0	0	0	0
	10–20	8	0	0	0	0
	20–30	13	0	0	0	0
	30–40	15	0	0	0.23	0.23
	>40	14	0	0	0	0

national park side of the border. All woody plants taller than 2.5 m with a main stem diameter > 5 cm at breast height were assessed for frequency of occurrence of recent uprooting, trunk snapping, or bark removal amounting to at least 50% of trunk circumference. About one third of all *Brachystegia boehmii* and one quarter of all *Burkea africana* trees with trunk diameters > 10 cm had been felled (either uprooted or with the main stem snapped) in the burned area, while substantially lower levels of such damage were recorded on the unburned side of the border (Table 1; tree nomenclature follows Gibbs Russell *et al.* 1984). From the size of the associated tracks, most of the tree felling had been done by female elephants.

A second observation, related to frost damage, was made following extremely low minimum temperatures recorded in Kasane in June (2 °C) and July (1 °C) 1994. Local felling of canopy trees was noticed in July 1994 while driving through the Kazuma Forest Reserve (location 25°31′E, 18°25′S). Nearby pans held pools of water, enabling some male elephants to remain in this region through the dry season. Recent severe damage inflicted by elephants was recorded in October 1994 within 11 belt transects 10 m × 400 m placed systematically to the west of the tarred road, plus another five transects east of the road. Frost damage to shrubs was recorded within randomly located patches of 10-m radius along each transect, noting the proportion of terminal stems of each shrub that appeared dead as a result of the frost.

Within the area sampled, over 50% of all *B. africana* and *B. boehmii* trees and over 40% of *Terminalia sericea* trees had recently been felled (Table 2). From 65% to 85% of the terminal stems of the majority of woody species in the shrub layer had been killed by frost, but with less damage recorded for *Combretum apiculatum* (39%), *Colophospermum mopane* (16%), *T. sericea* (7%) and *B. africana* (< 1%).

A third instance of localized severe damage to trees was associated with unusually low rainfall through March–April 1993, causing elephants to concentrate near the Linyanti River earlier than usual in the dry season. Observations were made in August 1993 in an area extending westwards of Linyanti Safari Camp (23°35′–23°47′E, 18°28′S). Within the riparian woodland, recent severe damage by elephants to three relatively common tree species was recorded within 20 belt transects measuring 10 m × 400 m, placed systematically 1 km apart perpendicular to the river. A further four sites were sampled within the adjoining mopane woodland where concentrated tree felling was noted. At each site observations were made within five 400 m × 15-m belt transects placed systematically 100 m apart. The

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Table 2. Severe damage to canopy trees inflicted by elephants in the Kazuma Forest Reserve following frosts during the dry season of 1994.

Species	Diameter class (cm)	n	Proportion of trees damaged: Uprooted	Stem snapped	Bark stripped > 50%	Overall
Burkea africana	5–10	6	0	0.33	0	0.33
	10–20	62	0.27	0.17	0	0.44
	20–30	97	0.52	0.08	0	0.60
	30–40	39	0.28	0.05	0	0.33
	40–50	9	0.22	0	0	0.22
Terminalia sericea	5–10	7	0	0.29	0	0.29
	10–20	51	0.16	0.26	0	0.42
	20–30	41	0.31	0.15	0	0.46
	30–40	3	0.33	0	0	0.33
Brachystegia boehmii	20–30	6	0.17	0.83	0	1.0
	30–40	20	0.1	0.6	0.05	0.75
	40–50	8	0	0.13	0.13	0.26
	>50	3	0	0.33	0	0.33

occurrence of recent severe damage was recorded for each tree > 5 cm in stem diameter.

In the riparian woodland, 79% of *Acacia nigrescens* trees, 60% of *Acacia erioloba* trees and 61% of *Terminalia prunioides* trees showed recent severe bark removal, but no recent felling was recorded in the transect sample because most trees were too large to be easily toppled. Nevertheless, we observed 11 trees being felled by male elephants over 6 d during September 1993. The felled trees included *Acacia luederitzii*, *Berchemia discolor*, *Boscia albitrunca*, *C. mopane*, *Peltophorum africanum* and *T. prunioides*, with stem diameters of 32–57 cm. Within local sites of heavy impact in the mopane woodland, over 50% of all *C. mopane* trees had been felled, including 25% of those 40–50 cm in stem diameter.

In all three situations, damage likely to result in the death of the tree affected 25–80% of canopy trees, and was inflicted within 1–10 wk. In savanna woodlands with elephants, rates of large tree mortality amounting to 1.5–6% y^{-1} have been sustained over periods of a decade or longer (Buechner & Dawkins 1961, Croze 1974, Tafangenyasha 1997, van de Vijver *et al.* 1999), reaching as high as 12–20% y^{-1} in specific localities (Buechner & Dawkins 1961, Field 1971). Although our study sites showed much greater tree mortality being imposed within less than a year, they represented small sections of the regional landscape.

The burn that occurred in the Kasane Forest Extension was the only instance of a fire during the 3-y duration of our study. We did not observe any other occurrences of canopy tree felling or frost damage either within our study area or along the road to Kasane which we drove repeatedly.

The common feature in two cases was a reduction in forage available within the shrub layer, which is normally favoured by elephants for feeding (Chafota 2007). Fire frequently kills much of the above-ground material of plants 2.5 m or less in height, but has little direct effect on larger trees, except in conjunction with bark removal by elephants (Laws *et al.* 1975) or porcupines (Yeaton 1988). Pienaar *et al.* (1966) noted that elephants may push over trees after a fire before leaving the area, while Laws (1970) suggested that the combined influences of elephants and fire on the shrub layer could lead to increased ring-barking of mature trees by elephants. Top-kill of shrubs by frost has been documented elsewhere in this region of south-central Africa (Childes & Walker 1987, Holdo 2006). In our study site, around 50% of the shoots that would otherwise have supplied forage for the elephants through the late dry season were eliminated. Nevertheless, some of the toppled trees showed no signs of feeding by elephants on the branch tips brought within reach.

In the Linyanti region, the early cessation of rain probably caused pools of water in the mopane-dominated hinterland to dry out earlier than usual. The consequently prolonged dependency of elephants on access to water from the river exacerbated the depletion of forage in the shrub layer of the riparian woodland. Heightened elephant impacts on woody plants near water during years with low rainfall have been recorded at Etosha in northern Namibia (de Beer *et al.* 2006). In our study site, much of the tree damage took the form of bark removal, and feeding occurred on all of the trees seen to be felled, indicating that food shortage rather than social display was responsible.

Localities where damage sufficient to cause the death of many trees had been inflicted by elephants, apparently within a brief period, are sometimes noted (Bell 2003, Owen-Smith pers. obs.), but with the cause remaining uncertain. Suggestions that these occurrences could in some cases result from social interactions among male elephants (Hendrichs 1971, Midgley *et al.* 2005) remain unsubstantiated. Our findings suggest that in some cases these events could arise via interactions with physical agents of disturbance, drastically reducing food availability in the shrub layer normally favoured by elephants. Holdo (2006) found that prior damage by frost had no consistent influence on the likelihood of these shrubs incurring subsequent damage from elephants, because species differed in their relative susceptibility to these agents. Furthermore, previously damaged stems were more likely to survive following new breakage by elephants than undamaged stems. However, the consequences of leaf or stem damage following frosts for the surrounding canopy trees were not reported. A simulation model developed using these findings suggested that elephants are the primary drivers of community structure and composition in Kalahari sand woodlands, and in interaction with fire and frost could promote the conversion of woodland into a shrub-dominated state (Holdo 2007).

However, neither the model developed by Holdo (2007) nor the approach by Baxter & Getz (2008) emphasizing elephant effects interacting with stochastic fire and rainfall conditions addressed consequences of spatial and temporal heterogeneity in these processes. Instead of leading to a progressive decline in canopy trees, lethal disturbances to canopy trees that are spatially concentrated while sufficiently widely spaced in time could promote a mosaic of patches in different stages of recovery, with rather different consequences for ecosystem diversity and function (Gilson 2004). Our observations suggest some mechanisms whereby a mosaic cycle of savanna woodland dynamics might be developed with elephants as the prime disturbing agent. A fundamental template for these interactions is provided by the distribution of surface water, constraining the regions of the broader landscape that elephants can occupy in high local densities under different conditions (Chammaille-Jammes *et al.* 2008). Further case studies are needed to establish how widely prevalent the episodic lethal disturbance to local stands of canopy trees that we apparently observed might be. Under certain conditions, the consequence could be greater regional diversity in woodland structure and composition than would prevail in the absence of elephants as a disturbing agent.

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LITERATURE CITED

BAXTER, P. W. J. & GETZ, W. M. 2008. Development and parameterization of a rain- and fire-driven model for exploring elephant effects in African savannas. *Environmental Modelling and Assessment* 13:221–242.

BELL, S. M. 2003. *Mortality rates of riparian woodland trees on the Linyanti River, northern Botswana*. M.Sc. research report, University of the Witwatersrand, Johannesburg.

BUECHNER, H. K. & DAWKINS, H. C. 1961. Vegetation change induced by elephants and fire in Murchison Falls National Park, Uganda. *Ecology* 42:752–766.

CHAFOTA, J. 2007. *Factors governing selective impacts of elephants on woody vegetation*. Ph.D. thesis, University of the Witwatersrand, Johannesburg.

CHAMMAILLE-JAMMES, S., FRITZ, H., VALEIX, M., MURINDAGOMO, F. & CLOBERT, J. 2008. Resource availability, aggregation and direct density dependence in an open context: the local regulation of an African elephant population. *Journal of Animal Ecology* 77:135–144.

CHILDES, S. L. & WALKER, B. H. 1987. Ecology and dynamics of the woody vegetation on Kalahari sands in Hwange National Park. *Vegetatio* 72:111–128.

CRAIG, G. C. 1990. Present population and distribution of elephants in northern Botswana. Pp. 16–18 in Hancock, P. (ed.). *The future of Botswana's elephants*. Gaborone, Botswana.

CROZE, H. 1974. The Seronera bull problem II. The trees. *East African Wildlife Journal* 12:29–47.

DE BEER, Y., KILIAN, W., VERSVELD, W. & VAN AARDE, R. J. 2006. Elephants and low rainfall alter woody vegetation in Etosha National Park, Namibia. *Journal of Arid Environments* 64:412–421.

DUBLIN, H. T., SINCLAIR, A. R. E. & MCGLADE, J. 1990. Elephants, fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology* 59:1147–1164.

FIELD, C. R. 1971. Elephant ecology in the Queen Elizabeth National Park, Uganda. *East African Wildlife Journal* 9:99–123.

GIBBS RUSSELL, G. E., GERMISHUIZEN, G., HERMAN, P., OLIVIER, P., PEROLD, S. M., REID, C., RETIEF, E., SMOOK, L., VAN ROOY, J. & WELMAN, W. G. 1984. *List of species of southern African plants*. Botanical Research Institute, Pretoria. 144 pp.

GIBSON, D. ST. C, CRAIG, G. C. & MASOGO, R. M. 1998. Trends of elephant population in northern Botswana from aerial survey data. *Pachyderm* 25:14–27.

GILSON, L. 2004. Evidence of hierarchical patch dynamics in an East African savanna? *Landscape Ecology* 19:883–894.

HENDRICHS, H. 1971. Freilandsbeobachtungen zum Sozialsystem der Afrikanischer Elefanten. Pp. 77–173 in Hendrichs, H. (ed.). *Dikdik und Elefanten*. R. Piper Verlag, Munich.

HIGGINS, S. J., BOND, W. J. & TROLLOPE, W. S. W. 2000. Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. *Journal of Ecology* 88:213–229.

HOLDO, R. M. 2006. Elephant herbivory, frost damage and topkill in Kalahari sand woodland savanna trees. *Journal of Vegetation Science* 17:509–518.

HOLDO, R. M. 2007. Elephants, fire, and frost can determine community structure and composition in Kalahari woodlands. *Ecological Applications* 17:558–568.

LAWS, R. M. 1970. Elephants as agents of habitat and landscape change in East Africa*Oikos* 21:1–15.

LAWS, R. M., PARKER, I. S. C. & JOHNSTONE, R. C. B. 1975. *Elephants and their habitats. The ecology of elephants in North Bunyoro, Uganda*. Oxford, Clarendon Press. 376 pp.

LEWIS, D. L. 1991. Observations of tree growth, woodland structure and elephant damage on *Colophospermum mopane* in Luangwa Valley, Zambia. *African Journal of Ecology* 29:207–221.

MAPAURE, I. N. & CAMPBELL, B. M. 2002. Changes in miombo woodland cover in and around Sengwa Wildlife Research Area, in relation to elephants and fire. *African Journal of Ecology* 40:212–219.

MIDGLEY, J. J., BALFOUR, D. & KERLEY, G. I. H. 2005. Why do elephants damage savanna trees? *South African Journal of Science* 101:213–215.

MOSUGELO, D. K., MORE, S. R., RINGROSE, S. & NELLEMANN, C. 2002. Vegetation changes during a 36-year period in northern Chobe National Park, Botswana. *African Journal of Ecology* 40:232–240.

PIENAAR, U. D. E. V., VAN WYK, P. & FAIRALL, N. 1966. An aerial census of elephant and buffalo in the Kruger National Park, and the implications thereof on intended management schemes. *Koedoe* 9:40–107.

REMMERT, H. 1991. The mosaic cycle of ecosystems – an overview. Pp. 1–21 in Remmert, H. (ed.). *The mosaic-cycle concept of ecosystems*. Springer-Verlag, New York.

SPINAGE, C. A. & GUINNESS, F. M. 1971. Tree survival in the absence of elephants in the Akagera National Park, Rwanda. *Journal of Applied Ecology* 8:723–728.

TAFANGENYASHA, C. 1997. Tree loss in the Gonarezhou National Park (Zimbabwe) between 1970 and 1983. *Journal of Environmental Management* 49:355–366.

VAN DE VIJVER, C. A. D. M., FOLEY, C. A. & OLFF, H. 1999. Changes in the woody component of an East African savanna during 25 years. *Journal of Tropical Ecology* 15:545–564.

WACKERNAGEL, A. 1993. *Elephants and vegetation: severity, scale and patchiness of impacts along the Linyanti river, Chobe District, Botswana*. M.Sc. thesis. University of the Witwatersrand, Johannesburg.

YEATON, R. I. 1988. Porcupines, fires and the dynamics of the tree layer of the *Burkea africana* savanna. *Journal of Ecology* 76:1017–1029.

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