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Nature and origin of tree and branch fall in the Taï Forest (Ivory Coast)

A. P. Vooren (Department of Silviculture, Agricultural University, P.O. Box 342, 6700 AH Wageningen, Netherlands)

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Abstract. Tree and branch fall modalities and their underlying causes varied considerably for canopy trees of different height classes in the tropical rain forest of the Taï National Park. Natural erosion played an important role in the uprooting of lower canopy trees, up to 25 m tall, while slender trees over 25 m tall were liable to be broken in their central stem parts by sudden squalls. Loss of branches occurred in trees which exhibited a high diameter/height ratio and was characteristic for senescent trees of the upper canopy.
Key words: Ivory Coast, tropical rain forest, mortality, dead trees, tree fall, uprooting.

Introduction. Death in a forest tree can take place as a sudden event – accidental death by external causes (cf. White, 1979) – or as a slowly progressing dieback process, i.e. senescence by internal causes. Such are, for instance, a decrease in metabolism and severe nutrient and water competition between the increasing numbers of sub-crowns (e.g. Hallé et al., 1978). The nature and suddenness of death influence the size of gap left in the forest canopy. An uprooted forest tree in general leaves the largest gap that can be created by a single tree fall. The tiniest gaps, on the contrary, occur with the slow dieback of a forest giant. In a forest where catastrophic disturbances caused by land-slides, earthquakes or storms are unusual events, as is the case in the Taï Forest, smaller and more frequent disturbances by falling canopy trees and branches become extremely important as intrinsic generators for the dynamics of new forest patches (e.g. Whitmore, 1982; Oldeman, 1983). Hence, it is of importance for a better understanding of forest regeneration processes to assess the different modalities of tree and branch fall, and to investigate the causes that trigger a specific type of fall.

Materials and methods. In 1981, a permanent study plot was set up in primeval forest in the Taï Biosphere Reserve, Ivory Coast. Within this 10-ha plot, which covered a slope of 500 m length from ridge top to valley bottom, fallen dead wood over 30 cm in diameter was mapped, measured, drawn to scale and tagged with plastic yellow labels. Fallen trees were classified as uprooted or broken-off. Their height of breakage and former total height were measured with a Suunto PH-5/15020 PC dendrometer. Trees were grouped according to their approximate total height in the classes 'smaller than 25 m', 'from 25 to 35 m' and 'over 35 m' (Table 1), to which is referred as 'low', 'middle' and 'upper' canopy ranges.

During a period of 3 years at approximately 6-month intervals the area was resurveyed by recording newly fallen trees, stems and branches of specimens over 30 cm dbh (diameter at breast height, ca. 1.3 m, or above higher-reaching buttresses or stilt roots).

Results. On a total of 95 entirely fallen trees, 31 (or 33 %) came down by uprooting (Table 1). The majority of uprooted trees (65 %) were less than 25 m tall and 8 out of these 20 trees clearly had been pulled down by falling neighbours. Another important agent for uprooting is natural erosion and this probably accounts for the high uprooting percentage in this forest as compared with the 17 % uprooting mentioned by Putz & Milton (1982) and the 25 % by Putz et al. (1983), both on Barro Colorado Island, Panama, or the 22 % by Florence (1981) at Makokou, Gabon. Besides gully erosion, which caused frequent uprooting events along its course, another typical uprooting erosion process appeared to exist in the marshy valley bottom and on its margins. Surface runoff water wears out a network of shallow streams on this rather flat sandy terrain, meandering around the bases of the larger trees (Fig. 1). This slow process of surface water erosion places medium-sized trees with their root systems on micro-hillocks. They topple over in a final stage. The latter event may be triggered by a loss of soil cohesion during heavy rainfall. A detailed description of this particular process, which seems to be confined to poorly drained soils, is given by Hütte (1968).

However, most of the entire fallen trees listed in table 1 came down by breakage of their basal stem parts. In a majority of cases the basal stem part, buttresses or root-swellings had rotted away in the moist contact zone with the soil. Moreover, 50 out of these 64 tree skeletons seemed to have descended in their full length in a sin-

Table 1. Mode of fall and height class distribution of fallen trees over 30 cm dbh in a 10-ha plot in the Taï Forest. Branch fall is indicated in numbers of branches.

Fallen trees over 30 cm dbh[1]	Tree height			Unknown	Total
	'low' (under 25 m)	'middle' (25 to 35 m)	'upper' (above 35 m)		
Fallen trees over 30 cm dbh					
uprooted	20	7	3	1	31
broken trunk at basal part	18	29	10	7	64
total	38	36	13	8	95
Fallen parts of trees over 30 cm dbh					
broken trunk at central part	21	13	5	–	39
broken trunk at distal part	3	–	–	–	3
branch fall	12	7	24	3	46
total	36	20	29	3	88

[1]dbh = diameter at breast height.

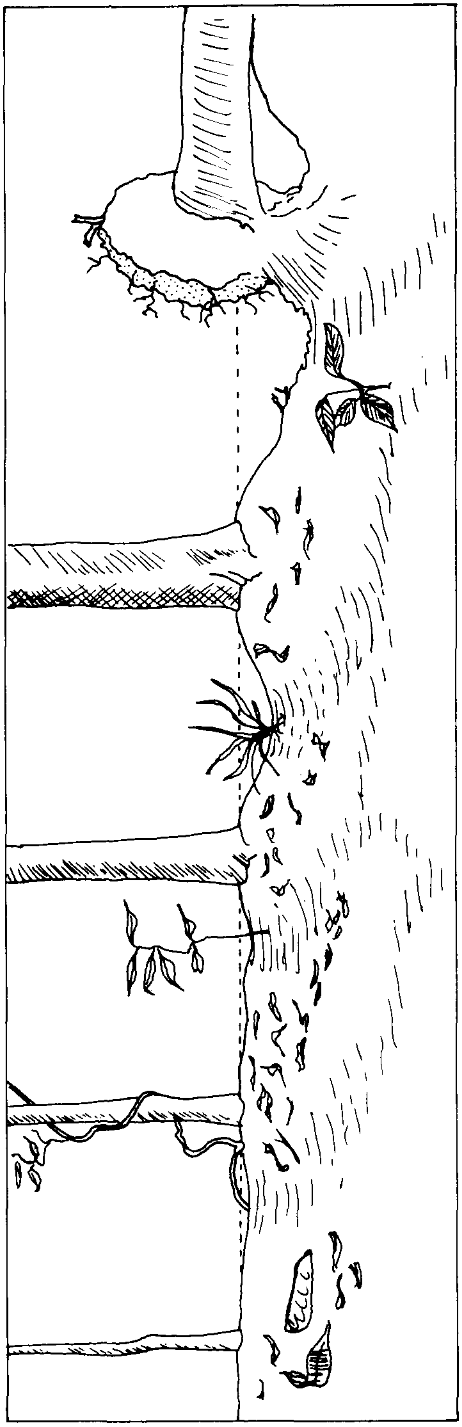

Fig. 1. Developmental series of micro-hillock formation by surface water erosion at the bases of middle-sized trees in the Tai Forest.

gle fall by succumbing of their bases. Only 8 trunks showed, by the wide dispersion of logs in different stages of decay, that they came down in a successive series of falls.

Trees listed in Table 1 as broken in their central stem parts exhibited a low diameter/height ratio. Their relative slenderness probably renders them vulnerable to strong wind gusts (cf. Jones, 1956; Brünig & Heuveldop, 1976). High diameter/height ratios for trees losing main branches, on the contrary, indicate that degradation of the main axis is especially liable to occur in over-mature trees which turn senescent. This tendency is less well marked in trees from lower storeys, the branches of which can be broken also by falling parts of taller trees.

Conclusions. The differences in the nature and origin of tree and branch fall, as exhibited by trees of the 'low', 'middle' and 'upper' canopy, may be reflected by varying mortality rates in these height classes (cf. Lang & Knight, 1983). The expression of the dynamic state of a forest in an average tree-fall or mortality rate should consistently account for a differential effect caused by unequal numbers of trees involved from the low, middle and upper canopy.

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This synopsis is based on Chapter 3.4 of a report by the same author entitled 'Patterns in tree and branch-fall in a West African rain forest', Report D85-05, Department of Silviculture, Agricultural University, Wageningen, 1985. iii + 34 pp., 13 figs, 5 tables, 149 refs., 10 appendices (photographs).

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The in sacco degradation of crude protein and cell wall constituents in grass, alfalfa and maize silages

R. P. Kwakkel[1,2], J. van Bruchem[1], G. Hof[2] and H. Boer[2] ([1]Department of Animal Physiology, Agricultural University, Haarweg 10, 6709 PJ Wageningen, Netherlands; [2]Department of Animal Nutrition, Agricultural University, Haagsteeg 4, 6708 PM Wageningen, Netherlands)

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Abstract. In the rumen of dairy cattle, fed on grasshay, the in sacco degradation was determined of crude protein (CP) and cell wall constituents (NDF) in grass, alfalfa (lucerne) and maize silages.

The silages were incubated for a 48-h period. The fractional rates of degradation were estimated based on a single exponential degradation model.

Key words: crude protein, in sacco, lignin, nylon bag, rumen, solubility, NDF.

Introduction. The nutritive value of roughages for ruminants is determined by both digestibility and voluntary intake. Roughage intake is primarily limited by the capacity of the rumen, the rate of degradation in the rumen and the passage rate of undegraded feed particles from the rumen.

Of these parameters, the rate of degradation can be determined in nylon bags incubated in the rumen for various periods of time, according to the method developed by Mehrez & Ørskov (1977).

The voluntary intake of the three silages was determined in steers (Hof et al., 1984). For grass, alfalfa (lucerne) and maize silages the daily intakes were 88.2, 105.2 and 85.8 g dry matter per $kg^{3/4}$, respectively. Of the grass and alfalfa silages, the digestion process in vivo was also studied in sheep fitted with ruminal and small intestinal cannulas (Kies et al., 1986).

In order to find an explanation for the differences in voluntary intake, the rate of degradation of cell wall constituents and crude protein was measured by the in sacco technique.

Material and methods. Samples (ca. 5 g dry matter) of the silages (particle length 0.5-1.5 cm) were incubated in nylon bags (nylon P41; 9 cm × 18 cm; pore size 41 μm