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Notes and Records

Role of even-age population structure in the disappearance of *Acacia xanthophloea* woodlands

Since the mid 1950s there has been a dramatic loss of *Acacia xanthophloea* Benth. (fever tree) woodland in Amboseli National Park in Kenya. Because fever trees are virtually the only canopy components of these woodlands, the deaths of large numbers of fever trees have had marked physiognomic and community consequences; as mature fever trees die and are not replaced promptly, woodland disappears. These changes have troubled both ecologists (Laws, 1970) and management authorities (Cowie, 1957).

Elephants (*Loxodonta africana* (Blumenbach)) in Amboseli, as elsewhere (Croze, 1974), may kill large fever trees (Western, 1973), and this activity is clearly a proximate cause of woodland disappearance. However, Western & van Praet (1973) recognized that some trees in Amboseli were dying without appreciable elephant damage, while apparently healthy trees were able to tolerate significant amounts of debarking and branch removal. Their study suggested that long-term climatic change was a more fundamental cause of tree mortality. They provided evidence that increased soil salinity, associated with a period of higher rainfall and a rising ground water-table in the closed drainage basin of Amboseli, produced a killing stress to many trees. Elephants then accelerated the process, as they fed in the groves of dead and weakened trees.

We suggest that the even-age stand structure of *A. xanthophloea* represents an even more fundamental cause of the sudden disappearance of fever tree woodland. When most of the adults of a population are the same, or nearly the same, age they will tend to senesce and die at around the same time (Stewart & Veblen, 1982). Whereas senescent death in a mixed-age stand is hardly noticeable, when senescence is synchronous, the population exhibits a dramatic dieback.

As plants senesce, they lose their ability to survive stress, and it has been proposed that environmental stresses act as enhancers of senescence (Noodén, 1980). Individuals in an even-age stand may survive a number of occasional stressful events when younger and more vigorous, but may all succumb to an event in itself no worse than the others, but which occurs after the trees have begun to senesce. Therefore, environmental stresses can act to synchronize cohort mortality in even-age stands. In Amboseli, climatic change and salinization may function in this way. Groves of even-aged mature fever trees have also been noted in Ngorongoro Crater (J. Kabigumila, pers. comm.) and Lake Manyara National Park, Tanzania (Weyerhaeuser, 1982), where both ground-water levels and elephant browsing have been implicated in their dynamics.

A similar interaction between age structure and climate has been suggested for mangroves (Jimenez, Lugo & Cintron, 1985). In mangrove stands that are characteristically monospecific or species poor, and where extensive disturbance has promoted the development of even-aged stands, the system's threshold to stress of its individual components is uniform. Stressors that exceed a critical level may thus trigger widespread tree mortality.

Although we are directing our attention to a particular kind of age-dependent mortality (senescence), the principle will apply as well to any size-specific mortality agent, such as soil chemistry below specific root depths, or vulnerability to windthrow above a given tree height. Size may be of equal or greater importance than absolute age in determining stand structure and subsequent fate in plants (Harper, 1977). Trees of varying age may be held at a similar size for an extended period by suppressing factors such as browsing, fire, or shade. When released, these trees mature together, forming stands of even size but dissimilar age. When a threshold size for the mortality agent is then reached, all the trees in the stand would be affected. *Acacia xanthophloea* may be less tolerant of repeated growth suppression than other *Acacia* species (Pellew, 1983), and thus size and age may be more closely correlated in this species.

Evidence of a relatively even-age stand structure in Amboseli fever trees was provided by Western & van Praet (1973), who cited the lack of extensive woodland in the mid to late 1800s and a 'relatively young woodland in the 1930s', with the major expansion occurring around the turn of the century. The stumps of trees that died in the 1960s and the remaining stands of adult trees show relatively uniform size distributions (Western, 1973; T. P. Young, pers. obs.), except along the margins of swamps in central Amboseli, and outside the Park, where soil salinity has remained low and where staggered cohorts have developed. *Acacia xanthophloea* is fast growing and has high reproductive rates, traits common in relatively short-lived trees. Tree cohorts starting early in this century would have been 50–60 years old at the onset of the observed dieback.

Climatic change and elephant feeding are probably secondary and tertiary causes, respectively, of fever tree woodland decline in Amboseli. Evidence that stand structure is a primary factor in the woodland disappearance is two-fold. Firstly, mature woodland has continued to die back in the central basin, while the water-table reportedly dropped in the 1970s and early 1980s (D. Western, pers. comm.) and was high again by 1984 (W. K. Lindsay, unpublished data). Secondly, even-aged stands of *A. xanthophloea* at Lakes Naivasha and Nakuru, 200 km north west of Amboseli, have experienced similar diebacks despite a number of historical lake level fluctuations no greater than in recent years, low soil salinity, and a complete absence of elephants. At Naivasha and Nakuru, the old, dying groves occur within a mosaic of healthier stands of different ages, while tree age and mortality in Amboseli appeared to be synchronized both within stands and between stands at similar distances from the basin centre.

A parallel case occurs in Hawaii, where the causes of dieback of stands of *Metrosideros polymorpha* Gaud. have been examined for many years (Mueller-Dombois *et al.*, 1983; Mueller-Dombois, 1983, 1985). Initial blame for the dieback was placed on pathogens, but later the critical importance of climate was realized. Only recently has it become clear that the most fundamental factor has been even-age stand structure, a principle that may also apply to many forest tree species studied in the Pacific region and in North America. As Mueller-Dombois *et al.* (1983, p. 130) sum up:

'a dieback mechanism is hereby suggested which involves (1) cohort senescence as the primary or predisposing cause, (2) sudden perturbation as a secondary and additionally synchronizing cause, acting as a trigger in the senescing life-stage, and (3) biotic agents as tertiary or contributing and dieback-hastening causes'.

This summary can be equally and appropriately applied to the disappearance of *A. xanthophloea* woodland and woodland patches. Even-age stands can occur in a number of other East African trees, including *Acacia tortilis* Forsk. (Weyerhaeuser, 1982), *Diospyros abyssinica* (Hiern) F. White (R. Lamprey, pers. comm.), *Melia volkensii* Gürke (W. Woodley, pers. comm.), and *Senecio keniodendron* R. E. & Th. Fries (Smith & Young, in press). The proximate environmental factors (e.g. shade, fire, browsing by a variety of herbivores, soil chemistry and water content) producing relative uniformity in the size/age distribution of trees may differ in particular cases, and might disrupt uniformity in other cases. Once stand structure has become homogeneous through the action of any single agent or combination of factors, however, the stage is set for size-specific stressors to generate synchronous mortality. Such simultaneous die-off may be limited to the trees within individual stands, or a higher level of synchrony may occur between separate stands in the same populaton, resulting in an even more striking shift in vegetation structure. Therefore, recognition of the long-term population and community consequences of even-age stands is likely to be important in our attempts to understand, manage, and conserve East African habitats.

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