The importance of "seed trees" for the natural regeneration of selectively logged tropical forest

ANDREW J. PLUMPTRE

Current address: Budongo Forest Project, PO Box 7298, Kampala, Uganda.

SUMMARY

Selective logging operations harvest trees above fixed diameter limits and therefore remove the largest trees which are likely to provide seed for the regeneration of the forest following harvesting. A study of several species of tree in the Budongo Forest in western Uganda showed that the percentage of trees fruiting at different diameters varies between species. For the mahoganies, *Khaya* and *Entandrophragma*, fruit production occurs at larger diameters than many of the other species. For these species the amount of fruit produced in areas of the forest exploited for timber is considerably less than in unlogged forest. Harvesting operations in Africa may remove the mahoganies as low as 50cm diameter and it is shown for three genera that seedling density is correlated with the density of trees above this diameter. The implications for forest management are discussed.

Key words: fruit production, DBH, sustainable logging, seedlings.

INTRODUCTION

Much of the current research on the fruiting of tropical trees concentrates on phenology (Van Schaik 1986, Newstrom, Frankie and Baker 1994), seed dispersal (Pannell 1989, Howe 1990, Chapman, Chapman and Wrangham 1992, Wrangham, Chapman and Chapman 1994), seed predation (Howe 1989, Schupp 1990) and seedling germination (Swaine and Whitmore 1988, Schupp 1990, Brown and Whitmore 1992). Where they have been carried out, phenological studies have mainly concentrated on the timing rather than the quantity of flower, fruit and leaf production (Van Schaik 1986, Levey 1990, Newstrom *et al.* 1994, White 1994). Part of the reason for this is a methodological one because most phenological studies have only recorded data from selected large trees whilst a measure of availability requires a study of the phenology of all sizes of tree. A few studies have attempted to quantify the production of fruit and/or leaves by relating the volume produced to the diameter at breast height (DBH) or basal area (DaSilva 1989, Chapman, Chapman, Wrangham, Hunt, Gebo and Gardner 1992, Greene and Johnson 1994). Even this has its methodological problems because the same tree can produce very different amounts of fruit from one year to the next (Newstrom *et al.* 1994, pers. obs.) so that DBH alone cannot be used as a good predictor of production.

Despite these difficulties the study of fruit production should be a necessary part of the sustainable management of tropical forests for timber for the following reasons. Where sustainable harvesting is being attempted, trees over a certain DBH are being removed at regular intervals. In addition trees pass through a juvenile phase when they do not produce any fruit and this tends to be prolonged in high forest because it protects the young tree from losing vigour during a period when vegetative growth is important (Heybroek 1974, Heybroek and Visser 1976). If it is a general rule that fruit production is correlated with DBH then the harvesting operations effectively remove the trees that produce most of the seed for subsequent crops (particularly if seed production is an increasing function of diameter). The effects of this reduced seed production may not be obvious for several felling cycles because of the time it takes for seedlings to reach an age for felling.

In order to investigate how selective logging might affect seed production in a tropical forest, a study of the fruiting of some of the important timber trees, and also those that are important for primates, was carried out in the Budongo Forest Reserve in western Uganda. This forest has been harvested on a sustainable yield basis since the mid 1920s with a cutting cycle of about 60 years. Initially enrichment planting of seedlings was undertaken but by the mid 1950s it was decided that this was uneconomic: most of the plantings died (Philip 1965). Consequently arboricide treatment was applied to open the canopy and encourage the natural regeneration of the mahoganies (*Khaya anthotheca* (Welw.) C.DC., *Entandrophragma angolense* (Welw.) C.DC., *E. cylindricum* (Sprague) Sprague and *E.utile* (Dawe and Sprague) Sprague. Eggeling (1947) and Synnott (1985) described the floristic composition of the forest and Philip (1965), Paterson (1991), Plumptre, Reynolds and Bakuneeta (1994) and Plumptre (in prep.) described the history of the management of the forest.

METHODS

Phenology

In each of eight compartments in the forest, five 2 km transects were cut as part of a primate censusing study (Plumptre and Reynolds 1994). At 100 metre intervals along these transects 7 metre radius circular plots were established and all trees over 10cm DBH marked for phenological data collection and the DBH recorded. A total of 5,640 trees were marked and monitored from January 1993 to January 1994. Each tree was visited twice each month and the amount of new leaves, ripe fruit, unripe fruit and flowers in the crown scored on a 0-4 scale (1=1-25% of crown with plant part, to 4=76-100%). This method was used because the study was designed to investigate changes in food availability for primates over the year. However, it provided a large enough sample size for the common trees to investigate the fruiting of different sizes of tree. The percentage of trees that produced fruit at least during one month was calculated for different diameter classes at 10 cm intervals up to 80 cm DBH and then in 20 cm intervals to 120 cm DBH for the following species:

Timber species:

1. *Khaya anthotheca* (Welw.) C.DC.
2. *Entandrophragma* spp. (all three species were lumped)
3. *Holoptelea grandis* (Hutch.) Mildbr.
4. *Maesopsis eminii* Engl.
5. *Chrysophyllum albidum* G. Don
6. *Chrysophyllum perpulchrum* Mildbr. ex Hutch.
7. *Antiaris toxicaria* (Pers.) Lesch.
8. *Albizia* spp (six species found in Budongo)

Primate food trees: (determined from visual observations)

1. *Strychnos mitis* S.Moore
2. *Funtumia elastica* (Preuss) Stapf
3. *Ficus sur* Forssk.
4. *Cynometra alexandri* C.H.Wright
5. *Celtis durandii* Engl.
6. *Celtis mildbraedii* Engl.
7. *Celtis zenkeri* Engl.
8. *Aningeria altissima* (A.Chev.) Aubrev. and Pellegr

These designations are fairly arbitrary because some of the timber species produce fruits that are eaten by primates (*Maesopsis*, *Chrysophyllum* and *Antiaris*) and some primate food trees are also used occasionally in Uganda as timber.

Forest inventory

During 1990 the Uganda Forest Department carried out an inventory of the common trees found in Budongo. A stratified random sampling strategy was used and trees of different sizes were recorded in nested plots as follows:

1. Two 5x5 metre plots - all seedlings and saplings < 10cm DBH
2. 50x10 metre plot - all trees >10cm DBH
3. 100x10 metre plot - all trees >20cm DBH
4. 100x50 metre plot - all trees >50cm DBH

A total of 467 plots were measured over the whole forest which sampled about 0.5% by area. For each plot the compartment, the forest type and whether it was exploited forest or not were recorded.

Analysis of fruit production

Chapman *et al.* (1992) found that DBH was linearly related to mass of fruit produced in several species of tree. Therefore the mean phenology score for each diameter class was multiplied by the midpoint of the diameter class to give a measure or score of fruit production (this multiplication included the effects of increasing size of the crown as DBH increases). Curves were fitted to plots of the score of fruit production against DBH to provide expected scores of fruit production at different DBH values. The inventory data provided stocking densities of the trees in each forest type for each diameter class. For this study the densities in mixed forest were used to compare fruit production between mixed exploited and mixed unexploited forest because mixed forest is the most common forest type in Budongo and is also where most of the mahoganies occur. Values of expected fruit production were multiplied by the density of trees for each diameter class to produce graphs where the area below the line gives a relative score of the production of fruit. These graphs provide comparisons for the same species in different areas but cannot usefully be used to compare between species.

Correlations between tree density and seedling density

The inventory data were used to correlate the density of seedlings and saplings in each compartment where more than three inventory plots were measured (<10cm DBH) with the density of trees greater than 10cm, 30cm, 50cm and 70cm DBH for *Khaya*, *Cynometra*, and *Chrysophyllum* as it was felt that the seedlings of these three species could be identified accurately.

RESULTS

Figure 1 plots the percentage of trees producing fruit against DBH for the main timber trees and Figure 2 does the same for the primate food trees. Curves have been fitted to the points by eye. From these it can be seen that *Entandrophragma* does not produce fruit until over about 80cm DBH and *Khaya* DBH must be about 40cm before it will fruit. Figure 3 plots the expected fruit production in unlogged and exploited mixed forest for some of these trees (*Celtis* and *Chrysophyllum* species were combined into generic classes in the inventory because it was not certain that the tree spotters were always accurate at distinguishing the species).

Plots were not continued beyond 100 cm DBH because the data on the fruiting patterns of trees above this size were based on low sample sizes (less than 4 trees). It is also possible that for some species large old trees show a decline in fruit production. Figure 3 shows that for the trees which fruit at low DBH values such as *Maesopsis*, *Funtumia* and *Celtis* (Figures 1 and 2) the amount of fruit produced in unlogged and exploited forest are similar (the areas shaded are similar). However, for *Khaya* and *Entandrophragma* the amount of fruit produced is reduced in the exploited forest. In the case of *Cynometra*, fruit production is reduced in the exploited forest because these trees were the focus of the arboricide treatment (Philip 1965). In general, primate food trees appear to be less affected by exploitation; this may partly explain why primates can occur at high densities in exploited forest (Plumptre and Reynolds 1994).

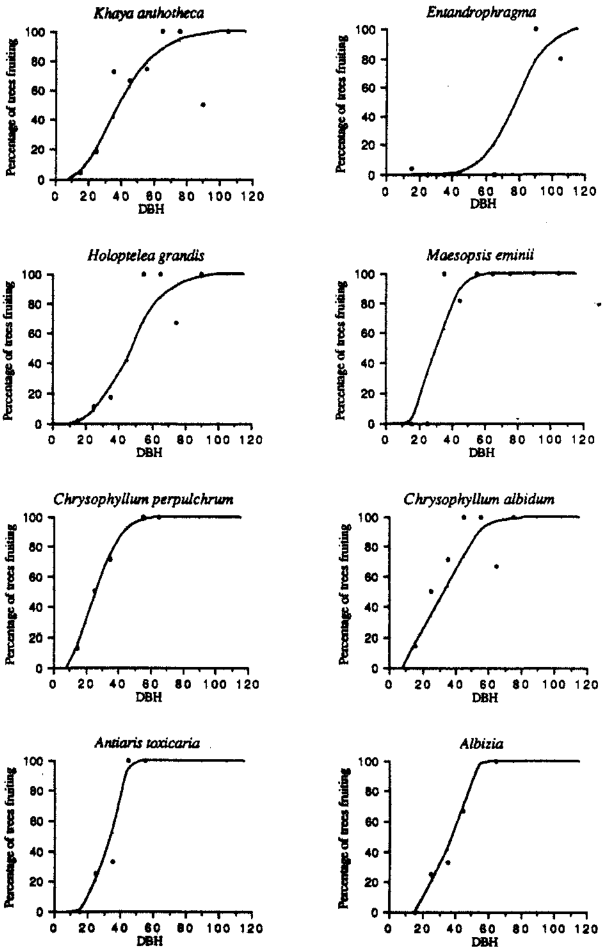

FIGURE 1. *The percentage of trees fruiting at different diameter classes for some of the main timber species found in Budongo.*

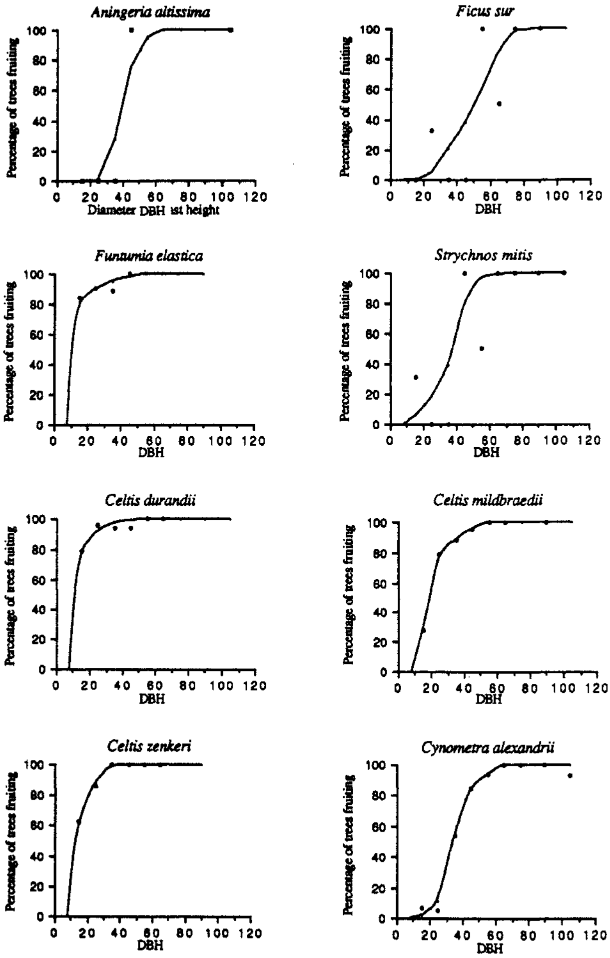

FIGURE 2. *The percentage of trees fruiting at different diameter classes for some of the species that produce fruit commonly eaten by primates.*

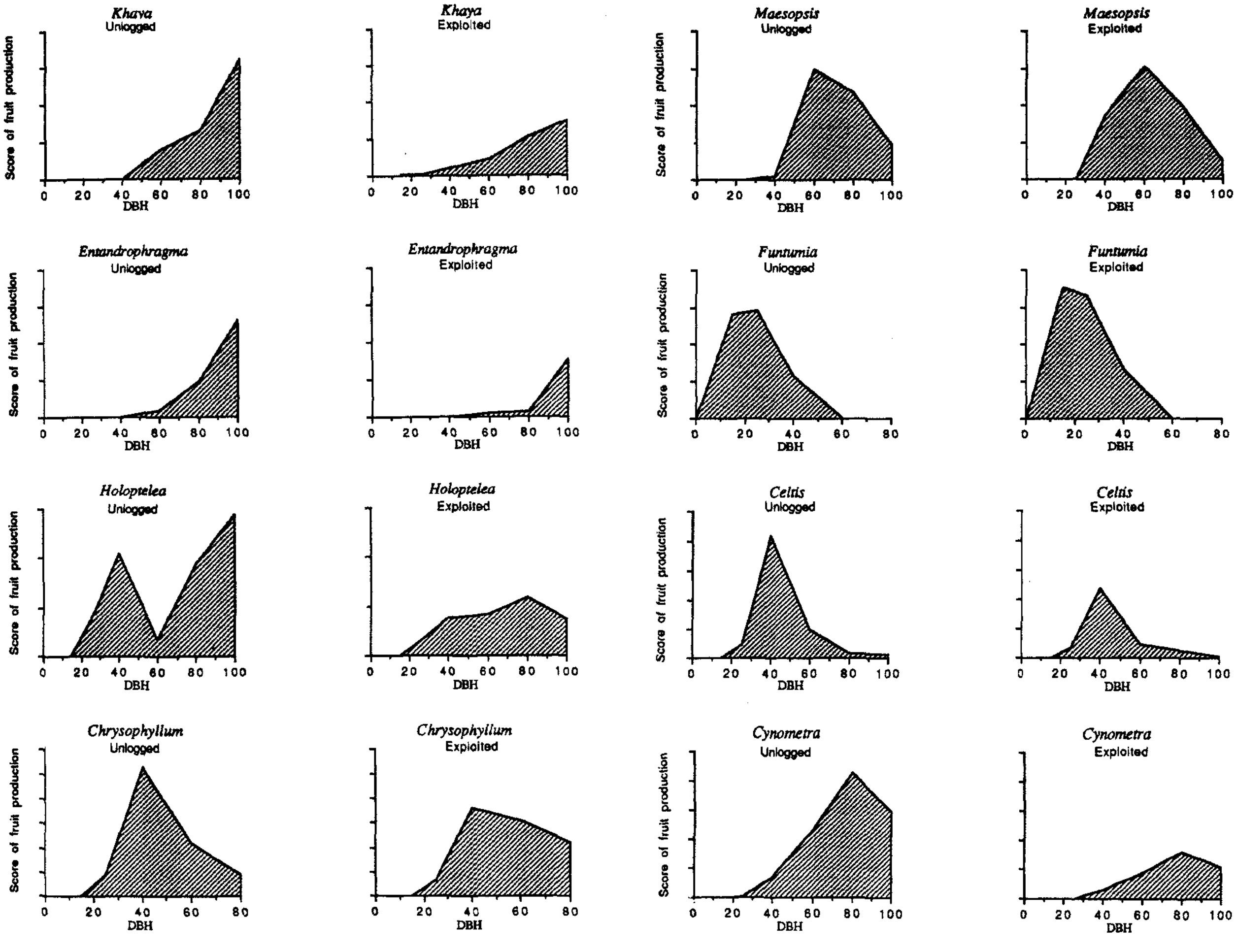

FIGURE 3. *The comparison of relative fruit production in unlogged and exploited mixed forest for eight trees. The score of fruit production is based on the number of trees of each size class and the product of the mean phenology score and mid DBH value of that size class.*

Table 1 gives the results of Pearson correlations between tree density and seedling density and the logarithm of seedling density. These show that the highest correlation for *Khaya* is between the density of trees above 50cm DBH and the logarithm of seedling density. This implies that the density of seedlings rises exponentially with an increase in the number of trees over 50 cm. For *Cynometra* and *Chrysophyllum* higher correlations are obtained from a linear increase in seedling density with large trees. The fact that all densities of *Cynometra* trees are significantly correlated with seedling density at all diameters may be due to this species tendency to form near monodominant stands where it occurs.

TABLE 1. *The correlation coefficients and significance levels between seedling density and density of trees greater than 10cm, 30cm, 50 cm and 70 cm. Correlations were calculated for seedling density (seedling) and natural logarithm of seedling density (lnSeedling). (*=P<0.01; **=P<0.001).*

Species	10cm	30cm	50cm	70cm
Khaya				
Seedling	0.199	0.458 *	0.600 **	0.588 **
lnSeedling	0.127	0.534 **	0.653 **	0.630 **
Cynometra				
Seedling	0.578 **	0.584 **	0.644 **	0.715 **
lnSeedling	0.519 **	0.518 **	0.572 **	0.646 **
Chrysophyllum				
Seedling	0.389 *	0.246	0.581 **	0.312
lnSeedling	0.330	0.220	0.501 **	0.243

DISCUSSION

Several assumptions were made in obtaining these results and these should be examined. Firstly it was assumed that the fruit production of the trees was related directly to DBH when producing the graphs in Figure 3. This assumption was based on previous work (Chapman *et al.* 1992) where this was shown to be true for certain understorey species of tree but it is possible that this is not the case for all of the species here. Secondly these results were obtained from only one year of phenological recordings and it is possible that for some species it was a poor year for fruit production. It might be found that in another year the number of trees fruiting at smaller sizes increases. Studies of fruiting in beech (*Fagus sylvatica*) showed that as DBH increased the number of years in which a tree fruited also increased (Kaplunovskii 1972). A study of dipterocarps in Malaysia showed that flowering occurred at lower DBH values in logged forest than in unlogged (Appanah and Manaf 1991) although in this study some of the dipterocarp species were different in the two sites. However, if the assumption that fruit production is related to DBH holds, neither of these observations will affect the results here greatly because most of the fruit is produced by the larger trees and there would have to be many smaller trees fruiting to add greatly to the volume of seed produced. This is probably why the higher correlations of seedling density with density of trees in Table 1 occur for large sized trees (although they may decrease for 70cm+ DBH where sample sizes were not so large).

In Budongo the harvesting of *Khaya* and *Entandrophragma* began in the 1920s with diameter limits of 120cm DBH. As harvesting progressed these were gradually reduced to the current 70cm (Philip 1965, Karani 1994). Consequently the production of fruit in exploited forest is probably higher than it might have been if trees had been removed at 70cm DBH from the start. As it is there is a considerable reduction in the relative amount of fruit as shown by the graphs for mahoganies in the exploited forest. The difference between the graphs for unlogged and exploited *Khaya* in Figure 3 are about 80 trees per square kilometre over 70 cm DBH or 0.8 per hectare. The felling practices in Budongo are fairly conservative, elsewhere felling may occur at 45 or 50cm DBH (Mohd 1992). At these diameters the production of fruit will decrease dramatically and in polycyclic logging systems there will not be sufficient time for some of the remaining trees to reach large sizes before the next cut. It is not known how important seedling number is for recruitment to adulthood. It is possible that high seedling densities are detrimental in some cases because they will attract predators or pathogens and lead to higher mortalities (Janzen 1970, Augspurger 1983, Augspurger and Kelley 1984). Synnott (1975) showed that mortality of *Entandrophragma* seedlings due to these agents was high in Budongo. However, it is better to produce too many rather than too few seedlings and it is suggested that measures are taken in the management of tropical forest to ensure high seed production. If the management of Budongo for timber is to rely on the natural regeneration of the *Khaya* spp. and *Entandrophragma* spp. for its next crop then some trees must be left as "seed trees" in each compartment. Alternatively there must be a programme of enrichment planting, possibly with larger seedlings than those used in the 1930s and 40s. Enrichment planting at this time was not very successful and was stopped in the 1950s due to the poor survival of seedlings and the costs (Philip 1965). There is some evidence that planting of 'striplings' (saplings that have had their leaves stripped off) in Budongo has been more successful (M.Byabazaire pers. comm.) and it is suggested that this should be investigated further.

These results show that care must be taken to ensure 'sufficient' seed production when attempting to manage tropical forest by natural regeneration. The effects of poor seed production may not be felt for several years on the supply of timber because of the time required for trees to reach harvestable diameters and consequently this aspect of the forest regeneration may not be monitored as closely. As it is not known how much seed is 'sufficient' for a reasonable recruitment of timber trees it is wise to produce many seeds until accurate estimates of seed and seedling mortality are produced. Seed production can vary greatly between years in the tropics with some trees failing to fruit completely in some years and therefore estimates of long-term seed production should be based on several years' data, not one year as it was here. If this aspect of seed production is ignored in the management of tropical forest for sustainable timber production it is predicted that the management objectives will not be achieved.

ACKNOWLEDGEMENTS

I would like to thank the ODA Forestry Research Programme, USAID and the Wildlife Conservation Society for funding this research and the Uganda Forest Department for the permission and support they gave me in Uganda. I also would like to thank the following Ugandan Field Assistants who helped me collect the data: Nabert Mutungire, Godfrey Biroch, Alfred Tholith, Julius Kyamanywa, Edison Lokiri, Martin Akanya, Stephen Hatari and James Kakura. Thanks also go to Professor G.A. Harrison, Dr V. Reynolds and V.De Newton for their help and use of facilities at the Institute of Biological Anthropology. Mr D. Sheil and an anonomous reviewer kindly provided comments on earlier drafts of this manuscript.

REFERENCES

APPANAH, S. and MANAF, M.R.A. 1991 Smaller trees can fruit in logged dipterocarp forests. *Journal of Tropical Forest Science* **3:** 80-87.

AUGSPURGER, C.K. 1983 Offspring recruitment around tropical trees :changes in cohort distance with time. *Oikos* **20:** 189-196.

AUGSPURGER, C.K. and KELLEY, C.K. 1984 Pathogen mortalityof tropical tree seedlings:experimental studies of the effects of dispersal distance, seedling density and light conditions. *Oecologia* **61:** 211-217.

BROWN, N.D. and WHITMORE, T.C. 1992 Do dipterocarp seedlings really partition tropical rain forest gaps? *Philosophical Transactions of the Royal Society* **335:** 369-378.

CHAPMAN, L.J., CHAPMAN, C.A. and WRANGHAM R.W. 1992 *Balanites wilsoniana* : elephant dependent dispersal? *Journal of Tropical Ecology* **8:** 275-283.

CHAPMAN, C.A., CHAPMAN, L.J., WRANGHAM, R.W., HUNT, K., GEBO, D. and GARDNER, L. 1992 Estimators of fruit abundance of tropical trees. *Biotropica* **24:** 527-531.

DASILVA, G.L. 1989 *The ecology of the western black and white colobus (*Colobus polykomos polykomos *Zimmerman) on a riverine island in south eastern Sierra Leone.* Unpublished D.Phil. thesis, University of Oxford.

EGGELING, W. 1947 Observations on the ecology of the Budongo rainforest, Uganda. *Journal of Ecology* **34:** 20-87.

GREENE, D.F. and JOHNSON, E.A. 1994 Estimating the mean annual seed production of trees. *Ecology* **75:** 642-647.

HEYBROEK, H.M. 1974 Selection pressures on tree populations in different plant formations. *Proceedings of Joint IUFRO-meeting* S02.04.1-3 Stockholm 1974, pp 271-282.

HEYBROEK, H.M. and VISSER, T. 1976 Juvenility in fruit growing and forestry. *Acta Horticulturae* **56:** 71-80.

HOWE, H.F. 1989 Scatter- and clump-dispersal and seedling demography: hypothesis and implications. *Oecologia* **79:** 417-426.

HOWE, H.F. 1990 Seed dispersal by birds and mammals: implications for seedling demography. *In:* Reproductive ecology of tropical forest plants (eds.) K.S.BAWA and M. HADLEY , pp 191-218. Parthenon Publishing group, UNESCO, Paris.

JANZEN, D.H. 1970 Herbivores and the number of tree species in tropical forests. *American Naturalist* **104:** 501-528.

KAPLUNOVSKII P.S. 1972 Fruiting behaviour in beech stands. *Lesoved.* **1:** 51-61.

KARANI, P.K. 1994 *Sustainable management of tropical rainforest in Uganda.* Commonwealth Secretariat, London.

LEVEY, D.J. 1990 Habitat-dependent fruiting behaviour of an understorey tree, *Miconia centrodesma*, and tropical treefall gaps as keystone habitats for frugivores in Costa Rica. *Journal of Tropical Ecology* **6:** 409-420.

MOHD, W.R.W. 1992 Silvicultural management issues limiting the quest for sustainability of natural tropical forests. Proceedings of the Tropical Silviculture Workshop, IUFRO Centennial Conference, 1992 Berlin, pp 15-24.

NEWSTROM, L.E., FRANKIE, G.W. and BAKER, H.G. 1994 A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. *Biotropica* **26:** 141-159.

PANNELL, C.M. 1989 The role of animals in natural regeneration and the management of equatorial rainforests for conservation and timber production. *Commonwealth Forestry Review* **68:**309-313

PATERSON, J.D. 1991 The ecology and history of Uganda's Budongo Forest. *Forest Conservation and History* **35:** 179-187.

PHILIP, M.S. 1965 Working Plan for the Budongo Central Forest Reserve. Third Revision 1964-1974. 130pp. Government Printer, Entebbe, Uganda.

PLUMPTRE, A.J. and REYNOLDS, V. 1994 The impact of selective logging on the primate populations in the Budongo Forest Reserve, Uganda. *Journal of Applied Ecology* **31:** 631-641.

PLUMPTRE, A.J., REYNOLDS, V. and BAKUNEETA, C. 1994 The contribution of fruit eating primates to seed dispersal and natural regeneration after selective logging. Report for ODA Forestry Research Program No.R4738.

SCHUPP, E.W. 1990 Annual variation in seedfall, postdispersal predation, and recruitment of a neotropical tree. *Ecology* **71:** 504-515.

SWAINE, M.D. and WHITMORE, T.C. 1988 On the definition of ecological species groups in tropical rainforests. *Vegetatio* **75:** 81-86.

SYNNOTT, T.J. 1975 Factors affecting the regeneration and growth of seedlings of *Entandrophragma utile* (Dawe and Sprague) Sprague. Unpublished Ph.D. thesis, Makerere University, Uganda. 275pp.

SYNOTT, T.J. 1985 A checklist of the flora of the Budongo Forest Reserve, Uganda, with notes on ecology and phenology. *CFI Occasional Paper* No. 27. Oxford Forestry Institute, Oxford.

VAN SCHAIK, C.P. 1986 Phenological changes in a Sumatran rain forest. *Journal of Tropical Ecology* **2:** 327-347.

WHITE, L.J.T. 1994 Patterns of fruit-fall phenology in the Lope reserve, Gabon. *Journal of Tropical Ecology* **10:** 289-312.

WRANGHAM, R.W., CHAPMAN, C.A. and CHAPMAN, L.J. 1994 Seed dispersal by forest chimpanzees in Uganda. *Journal of Tropical Ecology* **10:** 355-368.